SHOUT
SHARE
IT

DEPARTMENT OF COMMERCE
UNITED STATES OF AMERICA

Fishery Bulletin

Marine Biological Laboratory
LIBRARY
SEP 12 1980
Woods Hole, Mass.

Vol. 78, No. 1

ADAMS, PETER B. Life history patterns in marine fishes and their consequences for fisheries management 1

AMBLER, JULIE W. Species of *Munidopsis* (Crustacea, Galatheidae) occurring off Oregon and in adjacent waters 13

MENDELSSOHN, ROY. Using Markov decision models and related techniques for purposes other than simple optimization: analyzing the consequences of policy alternatives on the management of salmon runs 35

STOUT, VIRGINIA F. Organochlorine residues in fishes from the northwest Atlantic Ocean and Gulf of Mexico 51

PIETSCH, THEODORE W., and JOHN P. VAN DUZER. Systematics and distribution of ceratioid anglerfishes of the family Melanocetidae with the description of a new species from the eastern North Pacific Ocean 59

HUNTER, JOHN R., and CAROL M. KIMBRELL. Early life history of Pacific mackerel, *Scomber japonicus* 89

MORSE, WALLACE W. Spawning and fecundity of Atlantic mackerel, *Scomber scombrus*, in the Middle Atlantic Bight 103

WEIHS, DANIEL. Respiration and depth control as possible reasons for swimming of northern anchovy, *Engraulis mordax*, yolk-sac larvae 109

POWLES, HOWARD. Descriptions of larval silver perch, *Bairdiella chrysoura*, banded drum, *Larimus fasciatus*, and star drum, *Stellifer lanceolatus* (Sciaenidae) 119

GRIMES, CHURCHILL B., and GENE R. HUNTSMAN. Reproductive biology of vermilion snapper, *Rhomboplites aurorubens*, from North Carolina and South Carolina 137

PETERSON, R. H., P. H. JOHANSEN, and J. L. METCALFE. Observations on early life stages of Atlantic tomcod, *Microgadus tomcod* 147

Notes

HINES, ANSON H., and THOMAS R. LOUGHLIN. Observations of sea otters digging for clams at Monterey Harbor, California 159

WEIS, PEDDRICK, and JUDITH SHULMAN WEIS. Effect of zinc on fin regeneration in the mummichog, *Fundulus heteroclitus*, and its interaction with methylmercury 163

(Continued on back cover)

Seattle, Washington

U.S. DEPARTMENT OF COMMERCE
Philip M. Klutznick, *Secretary*

NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION
Richard A. Frank, *Administrator*
Terry L. Leitzell, *Assistant Administrator for Fisheries*

NATIONAL MARINE FISHERIES SERVICE

Fishery Bulletin

The *Fishery Bulletin* carries original research reports and technical notes on investigations in fishery science, engineering, and economics. The Bulletin of the United States Fish Commission was begun in 1881; it became the Bulletin of the Bureau of Fisheries in 1904 and the Fishery Bulletin of the Fish and Wildlife Service in 1941. Separates were issued as documents through volume 46; the last document was No. 1103. Beginning with volume 47 in 1931 and continuing through volume 62 in 1963, each separate appeared as a numbered bulletin. A new system began in 1963 with volume 63 in which papers are bound together in a single issue of the bulletin instead of being issued individually. Beginning with volume 70, number 1, January 1972, the *Fishery Bulletin* became a periodical, issued quarterly. In this form, it is available by subscription from the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402. It is also available free in limited numbers to libraries, research institutions, State and Federal agencies, and in exchange for other scientific publications.

EDITOR

Dr. Jay C. Quast
Scientific Editor, *Fishery Bulletin*
Northwest and Alaska Fisheries Center
Auke Bay Laboratory
National Marine Fisheries Service, NOAA
P.O. Box 155, Auke Bay, AK 99821

Editorial Committee

Dr. Elbert H. Ahlstrom
National Marine Fisheries Service

Dr. Bruce B. Collette
National Marine Fisheries Service

Dr. Edward D. Houde
University of Miami

Dr. Merton C. Ingham
National Marine Fisheries Service

Dr. Reuben Lasker
National Marine Fisheries Service

Dr. Jerome J. Pella
National Marine Fisheries Service

Dr. Sally L. Richardson
Gulf Coast Research Laboratory

Kiyoshi G. Fukano, Managing Editor

The *Fishery Bulletin* (USPS 090-870) is published quarterly by Scientific Publications Office, National Marine Fisheries Service, NOAA, Room 336, 1700 Westlake Avenue North, Seattle, WA 98109. Controlled circulation paid to Finance Department, USPS, Washington, DC 20260.

Although the contents have not been copyrighted and may be reprinted entirely, reference to source is appreciated.

The Secretary of Commerce has determined that the publication of this periodical is necessary in the transaction of the public business required by law of this Department. Use of funds for printing of this periodical has been approved by the Director of the Office of Management and Budget through 31 March 1982.

Fishery Bulletin

CONTENTS

Vol. 78, No. 1

ADAMS, PETER B. Life history patterns in marine fishes and their consequences for fisheries management 1
AMBLER, JULIE W. Species of *Munidopsis* (Crustacea, Galatheidae) occurring off Oregon and in adjacent waters 13
MENDELSSOHN, ROY. Using Markov decision models and related techniques for purposes other than simple optimization: analyzing the consequences of policy alternatives on the management of salmon runs 35
STOUT, VIRGINIA F. Organochlorine residues in fishes from the northwest Atlantic Ocean and Gulf of Mexico 51
PIETSCH, THEODORE W., and JOHN P. VAN DUZER. Systematics and distribution of ceratioid anglerfishes of the family Melanocetidae with the description of a new species from the eastern North Pacific Ocean 59
HUNTER, JOHN R., and CAROL M. KIMBRELL. Early life history of Pacific mackerel, *Scomber japonicus* 89
MORSE, WALLACE W. Spawning and fecundity of Atlantic mackerel, *Scomber scombrus*, in the Middle Atlantic Bight 103
WEIHS, DANIEL. Respiration and depth control as possible reasons for swimming of northern anchovy, *Engraulis mordax*, yolk-sac larvae 109
POWLES, HOWARD. Descriptions of larval silver perch, *Bairdiella chrysoura*, banded drum, *Larimus fasciatus*, and star drum, *Stellifer lanceolatus* (Sciaenidae) 119
GRIMES, CHURCHILL B., and GENE R. HUNTSMAN. Reproductive biology of vermilion snapper, *Rhomboplites aurorubens*, from North Carolina and South Carolina 137
PETERSON, R. H., P. H. JOHANSEN, and J. L. METCALFE. Observations on early life stages of Atlantic tomcod, *Microgadus tomcod* 147

Notes

HINES, ANSON H., and THOMAS R. LOUGHLIN. Observations of sea otters digging for clams at Monterey Harbor, California 159
WEIS, PEDDRICK, and JUDITH SHULMAN WEIS. Effect of zinc on fin regeneration in the mummichog, *Fundulus heteroclitus*, and its interaction with methylmercury 163

(Continued on next page)

Seattle, Washington

1980

For sale by the Superintendent of Documents, U. S. Government Printing Office, Washington, DC 20402—Subscription price per year: $12.00 domestic and $15.00 foreign. Cost per single issue: $3.00 domestic and $3.75 foreign.

TESTAVERDE, SALVATORE A., and JAMES G. MEAD. Southern distribution of the Atlantic whitesided dolphin, *Lagenorhynchus acutus*, in the western North Atlantic 167
MATARESE, ANN C., and DAVID L. STEIN. Additional records of the sculpin *Psychrolutes phrictus* in the eastern Bering Sea and off Oregon 169
ODELL, DANIEL K., EDWARD D. ASPER, JOE BAUCOM, and LANNY H. CORNELL. A recurrent mass stranding of the false killer whale, *Pseudorca crassidens*, in Florida 171
BRANSTETTER, STEVEN, and ROBERT L. SHIPP. Occurrence of the finetooth shark, *Carcharhinus isodon*, off Dauphin Island, Alabama 177
BAGLIN, RAYMOND E., JR., MARK I. FARBER, WILLIAM H. LENARZ, and JOHN M. MASON, JR. Shedding rates of plastic and metal dart tags from Atlantic bluefin tuna, *Thunnus thynnus* 179
HAYNES, JAMES M., and ROBERT H. GRAY. Influence of Little Goose Dam on upstream movements of adult chinook salmon, *Oncorhynchus tshawytscha* 185
MORSE, WALLACE W. Maturity, spawning, and fecundity of Atlantic croaker, *Micropogonias undulatus*, occurring north of Cape Hatteras, North Carolina 190
MILLER, ROBERT E., DOUGLAS W. CAMPBELL, and PAMELA J. LUNSFORD. Comparison of sampling devices for the juvenile blue crab, *Callinectes sapidus* ... 196

Notices

NOAA Technical Reports NMFS published during the last 6 mo of 1979 199

Vol. 77, No. 4 was published on 23 July 1980.

The National Marine Fisheries Service (NMFS) does not approve, recommend or endorse any proprietary product or proprietary material mentioned in this publication. No reference shall be made to NMFS, or to this publication furnished by NMFS, in any advertising or sales promotion which would indicate or imply that NMFS approves, recommends or endorses any proprietary product or proprietary material mentioned herein, or which has as its purpose an intent to cause directly or indirectly the advertised product to be used or purchased because of this NMFS publication.

LIFE HISTORY PATTERNS IN MARINE FISHES AND THEIR CONSEQUENCES FOR FISHERIES MANAGEMENT

PETER B. ADAMS[1]

ABSTRACT

Natural selection operates at the life history level to maximize the number of surviving offspring. Life history characteristics will vary in consistent patterns to meet this constraint. When theoretical patterns in life histories were investigated in terms of r and K selection and compared with actual trends in life history characteristics of fishes, the agreement between observed and predicted trends was significant. The effects of harvesting on stocks with these life history trends were investigated and it was found that K selected type species would be highly sensitive to overfishing and, once depleted, recovery would require a long time.

The ecological and genetic properties of a species are intimately linked. The morphological and reproductive characteristics, population sizes, and genetic frequencies of species are adjusted to their environments by natural selection. Species inhabiting different environments show different patterns of life history characteristics. The relationship among habitat, ecological strategies, and population parameters has been termed r and K selection (MacArthur and Wilson 1967) and/or optimal life histories (Gadgil and Bossert 1970). This body of theory is based on the assumption that natural selection operates on these characteristics in order to maximize the number of surviving offspring produced. Under an environmental regime with a large component of unpredictable, nonselective, mortality an organism will allocate a larger portion of its resources to reproductive activities (an r strategist). Conversely the optimal allocation of resources for a population subjected to a high proportion of predictable, selective mortality will be toward increasing individual fitness, frequently through competitive ability (a K strategist). With the number and variability of factors operating on any particular species, no species is going to be an r or K strategist in an absolute sense. A species will only occupy a relative position on the r and K continuum.

In fisheries biology, the value of comparative studies of life history parameters has long been recognized (Holt 1962; Beverton 1963; Cushing 1971; Alverson and Carney 1975). These life history parameters should vary in a consistent pattern which can be predicted from the theory of r and K selection. In this paper, these predictions are tested with life history parameters from major groups of marine fishes. The theory has implications for management, particularly when fisheries are in the initial stages of development.

THEORY OF r AND K SELECTION

The theory of r and K selection is based on two assumptions about the allocation of a population's resources between competitive and reproductive functions (Pianka 1974; Gadgil and Bossert 1970; Schaffer and Gadgil 1975). The first is that there is a positive relationship between the amount of resources spent on an offspring and the fitness of that offspring. The second assumption is that any species only has a fixed amount of resources available. This results in an inverse relationship between the number of offspring produced and their average fitness. The criterion for success in natural selection is the number of surviving offspring that a parent produces (Crow and Kimura 1970). Therefore, the best reproductive strategy is a compromise between two conflicting demands: production of the largest possible total number of offspring (r selection), and production of offspring with the highest possible fitness (K selection). The particular point of compromise for any species will be a function of the selection factors operating on that species and would be that species' position on the r and K continuum.

The second part of the theory concerns the relationship between these life history strategies and

[1] Southwest Fisheries Center Tiburon Laboratory, National Marine Fisheries Service, NOAA, Tiburon, CA 94920.

Manuscript accepted September 1979.
FISHERY BULLETIN: VOL. 78, NO. 1, 1980.

the habitat the species occupies (Southwood et al. 1974; Southwood and Comins 1976). If mortality factors in an environment are variable and/or unpredictable, then their effects are likely to be less selective in terms of population size or of the phenotype involved. Under these circumstances, individual competitive fitness is of relatively less importance. The best strategy would be to place maximal resources into reproduction and produce as many offspring as possible (r selection).

The contrasting situation is an environment in which mortality factors are stable and/or predictable. Mortality under these circumstances will result in strong selection for individual fitness and there will be pronounced differences between their effects on different phenotypes. In these stable environments, the optimal strategy would be to produce offspring with substantial competitive ability (K selection). Due to the previously assumed relationship between fitness per offspring and the number of offspring produced, this also means the production of fewer offspring.

The two situations described above are end points of a spectrum. Species will always have a number of different selective pressures operating on them, both spatially and temporally. This is particularly evident in aquatic organisms which characteristically go through several life history stages. This again emphasizes that the concept of r and K selection should be applied only in a comparative sense. Finally, comparisons must be made between species of a similar ecological nature. Comparisons between species of different ecological types is meaningless since fundamentally different types of selective factors will be operating in those cases.

r AND K SELECTION IN MARINE FISHES

Natural selection will favor nonreproductive activities at the expense of reproductive activities only when they enhance reproduction at later stages in the life history and thereby maximize overall survival (Crow and Kimura 1970). Changes in allocation of a species' resources from reproductive to competitive activities will only occur in habitats where competitive activities enhance the survival of future offspring. The result of this is that organisms under different selection pressures will have characteristic life history patterns. An r selected species will have life history strategies which tend toward productivity. The K selected species will have life strategies which tend toward efficient exploitation of a specific limiting resource (Pianka 1974). Therefore, specific combinations of population parameters can be identified as being characteristic of an r strategist, while the opposing combination would be characteristic of a K strategist.

A species which is exposed to a large component of nonselective or catastrophic mortality (i.e., an r strategist) would be selected for characteristics that would increase productivity. Increasing productivity through reproductive activity generally implies: 1) early maturity, 2) rapid growth rates, 3) production of larger numbers of offspring at a given parental size, and 4) maximum production of offspring at early age (Gadgil and Bossert 1970). Other characteristics which are results of the allocation of large portions of resources to reproductive activity are: 1) small body size, 2) high rates of mortality, and 3) shorter life span (Pianka 1974; Gadgil and Solbrig 1972). In terms of commonly measured population parameters in fishery biology, an r selected species would have: 1) a low age at first maturity, 2) a high value of k from the von Bertalanffy growth equation, 3) a small L_∞ from the von Bertalanffy growth equation, 4) high rates of instantaneous natural mortality (M), and 5) low maximum age.

Even in environments with predictable mortality sources, increased allocation of resources to competitive activities will only occur when two prerequisites are met (Schaffer and Gadgil 1975). The first is that reproductive potential increases with some function of age. The second is that there is some additional mortality risk associated with reproduction. Under these assumptions, the attributes associated with a K strategist would be: 1) delayed maturity, 2) reduced growth rates, 3) low mortality rates, 4) large body size, and 5) longer life span. Again in terms measured in fishery biology, a K selected species would have: 1) a high age at first maturity, 2) a low k from the von Bertalanffy growth equation, 3) a large L_∞ from the von Bertalanffy growth equation, 4) low M, and 5) a high maximum age.

Using these life history correlates of r and K selection (summarized in Table 1), it is possible to predict the signs of a correlation matrix between life history parameters (Table 2). The predicted matrix can be compared with actual matrices calculated using Spearman's rank correlation coefficient. This coefficient only assumes that the observed data are mutually independent and come

TABLE 1.—Summary of hypothetical r and K correlates in life history parameters of fishes.

Characteristics	r selected	K selected
Body size, L_∞[1]	Small	Large
Maximum age	Low	High
Age at first maturity	Low	High
Natural mortality, M	High	Low
Growth rate, k[1]	High	Low

[1]The parameter from the von Bertalanffy growth equation was used to represent the actual characteristic.

TABLE 2.—Predicted signs of correlation matrix of life history parameters in fishes.

Characteristics	L_∞[1]	Maximum age	Age at first maturity	M	k[1]
Body size, L_∞[1]	1.0	-	+	-	-
Maximum age		1.0	+	-	-
Age at first maturity			1.0	-	-
Natural mortality, M				1.0	+
Growth rate, k[1]					1.0

[1]The parameter from the von Bertalanffy growth equation was used to represent the actual characteristic.

from a continuous bivariate population (Hollander and Wolfe 1973).

RESULTS

Life history parameters were gathered from the literature for several major groups of marine fishes. Often there were multiple sets of data for the same species from different locations. Each set of values was used as a separate data case. The literature citations for the actual parameters are listed by group in Appendix I. Correlation matrices were calculated for the following groups of fish: 1) herring and anchovies, Clupeidae and Engraulidae (Table 3), 2) salmons, Salmonidae (Table 4), 3) cods, Gadidae (Table 5), 4) rockfishes, Scorpaenidae, genus *Sebastodes* (Table 6), and 5) flatfishes, Pleuronectiformes (Table 7).

All of the observed correlations agree with the predicted correlations in sign (Table 8). Of the observed correlations, 40 of a possible 46 (or 87%) were significantly different from zero at a 5% probability level. If the observed correlation agreement of coefficients were distributed ran-

TABLE 3.—Correlation coefficients between life-history parameters for herring and anchovies (families Clupeidae and Engraulidae). For sources of data see Appendix I. The number in parentheses represents the significance value for that particular coefficient since the number of data cases was different for each correlation.

Characteristics	L_∞[1]	Maximum age	Age at first maturity	M	k[1]
Body size, L_∞[1]	1.0	0.846 (0.001)	0.816 (0.001)	−0.746 (0.001)	−0.720 (0.001)
Maximum age		1.0	0.904 (0.001)	−0.797 (0.001)	−0.763 (0.001)
Age at first maturity			1.0	−0.702 (0.001)	−0.732 (0.001)
Natural mortality, M				1.0	0.876 (0.001)
Growth rate, k[1]					1.0

[1]The parameter from the von Bertalanffy growth equation was used to represent the actual characteristic.

TABLE 4.—Correlation matrix between life-history parameters for salmons (family Salmonidae). For sources of data see Appendix I. The number in parentheses represents the significance value for that particular coefficient since the number of data cases was different for each correlation.

Characteristics	L_∞[1]	Maximum age	Age at first maturity	M	k[1]
Body size, L_∞[1]	1.0	0.765 (0.001)	0.728 (0.032)	−0.785 (0.001)	−0.730 (0.002)
Maximum age		1.0	0.776 (0.020)	−0.737 (0.003)	−0.674 (0.004)
Age at first maturity			1.0	−0.644 (0.084)	−0.812 (0.013)
Natural mortality, M				1.0	0.896 (0.001)
Growth rate, k[1]					1.0

[1]The parameter from the von Bertalanffy growth equation was used to represent the actual characteristic.

TABLE 5.—Correlation matrix between life-history parameters for cods (family Gadidae). For sources of data see Appendix I. The number in parentheses represents the significance value for that particular coefficient since the number of data cases was different for each correlation.

Characteristics	L_∞[1]	Maximum age	Age at first maturity	M	k[1]
Body size, L_∞[1]	1.0	0.795 (0.002)	0.833 (0.001)	−0.647 (0.022)	−0.666 (0.001)
Maximum age		1.0	0.737 (0.014)	−0.654 (0.028)	−0.702 (0.008)
Age at first maturity			1.0	−0.715 (0.035)	−0.658 (0.008)
Natural mortality, M				1.0	0.950 (0.001)
Growth rate, k[1]					1.0

[1]The parameter from the von Bertalanffy growth equation was used to represent the actual characteristic.

TABLE 6.—Correlation matrix between life-history parameters for rockfishes (family Scorpaenidae, genus *Sebastodes*). For sources of data see Appendix I. The number in parentheses represents the significance value for that particular coefficient since the number of data cases was different for each correlation.

Characteristics	L_∞[1]	Maximum age	Age at first maturity	k[1]
Body size, L_∞[1]	1.0	0.662 (0.019)	0.456 (0.088)	−0.490 (0.075)
Maximum age		1.0	0.612 (0.030)	−0.567 (0.040)
Age at first maturity			1.0	−0.651 (0.021)
Growth rate, k[1]				1.0

[1]The parameter from the von Bertalanffy growth equation was used to represent the actual characteristic.

TABLE 7.—Correlation matrix between the life-history parameters for flatfishes (order Pleuronectiformes). For sources of data see Appendix I. The number in parentheses represents the significance value for that particular coefficient since the number of data cases was different for each correlation.

Characteristics	L_∞[1]	Maximum age	Age at first maturity	M	k[1]
Body size, L_∞[1]	1.0	0.755 (0.001)	0.956 (0.001)	−0.291 (0.156)	−0.619 (0.005)
Maximum age		1.0	0.824 (0.001)	−0.355 (0.142)	−0.808 (0.001)
Age at first maturity			1.0	−0.630 (0.014)	−0.732 (0.001)
Natural mortality, M				1.0	0.367 (0.098)
Growth rate, k[1]					1.0

[1]The parameter from the von Bertalanffy growth equation was used to represent the actual characteristic.

TABLE 8.—Summary of the number of agreements between predicted and observed correlation coefficients among life-history parameters within selected taxonomic groups.

Level of agreement	Number in agreement	Number possible	Percent in agreement
Sign	46	46	100
5% probability level	40	46	87
1% probability level	31	46	67

domly (i.e., p = probability of agreement = 0.5, and q = probability of disagreement = 0.5), then the number of agreements would follow a binomial distribution. The binomial test (Hollander and Wolfe 1973) can be used to test the hypothesis that the number of agreements between the predicted and observed correlations differs from the number that would have occurred randomly. The number of agreements is significantly different than would have occurred randomly ($z = 4.86$, $P<0.001$), when only correlations that were significant at the 5% level were used.

RESPONSE OF r AND K SELECTED SPECIES TO HARVESTING

The interaction of life history characteristics will have a strong affect on the response of a species to fishing pressure. The Beverton and Holt yield per recruit equation estimates the yield that can be harvested from the growth of a cohort. The model assumes that fish growth is described by the von Bertalanffy growth curve and that mortality processes are exponential (Beverton and Holt 1957; Ricker 1975). The biological parameters in the model are: 1) M, the instantaneous rate of natural mortality, 2) W_∞, the mean asymptotic weight which corresponds to L_∞, 3) k, the von Bertalanffy growth coefficient, and 4) t_λ, the maximum age of a fish. From r and K selection, we can predict how these parameters will vary. Consider a situation with three hypothetical species: one species will be more r selected, another species will be more K selected, and another will be intermediate between the first two. The biological parameters will vary as shown in Table 9. Beverton and Holt yield per recruit curves were calculated for a constant age at first capture ($t_r = 4.2$ yr) with varying fishing mortality (Figure 1), and for a constant fishing mortality ($F = 0.25$) with a varying age at first capture (Figure 2).

The yield per recruit analysis points up that there are specific differences in fisheries based on r or K selected species. In fisheries based on K selected species, the maximum yield per recruit would occur at a lower level of fishing mortality and at a later age at first entry than in fisheries based on r selected species. The curves also indicate that K selected species would be much more sensitive to overfishing both in terms of fishing mortality and age at first entry.

The surplus production model of Schaefer combines reproductive and mortality functions into one parameter (Ricker 1975). The biological parameters in this model are B_∞, the maximum stock size (or carrying capacity in weight), and k, the instantaneous rate of increase of the stock at densities approaching zero. Again these parameters can be predicted for the three hypothetical species from r and K selection (Table 10). In the surplus production model analysis (Figure 3), the r selected species have the highest productivity. As in the yield per recruit analysis, the maximum yield occurs at a lower fishing mortality for the K

TABLE 9.—Biological parameters for use in yield per recruit analysis for three hypothetical r and K selected species.

Biological parameters	r selected species	Intermediate species	K selected species
Natural mortality, M	0.30	0.20	0.10
Mean asymptotic weight, W_∞	641 g	1,141 g	1,641 g
von Bertalanffy growth coefficient, k	0.22	0.14	0.07
Maximum age, t_λ	13 yr	20 yr	35 yr

TABLE 10.—Biological parameters for surplus production model analysis for three hypothetical r and K selected species.

Biological parameters	r selected species	Intermediate species	K selected species
Maximum stock size (B_∞)	1.54×10^8g	2.04×10^8g	2.54×10^8g
Rate of increase (k)	0.912	0.612	0.312

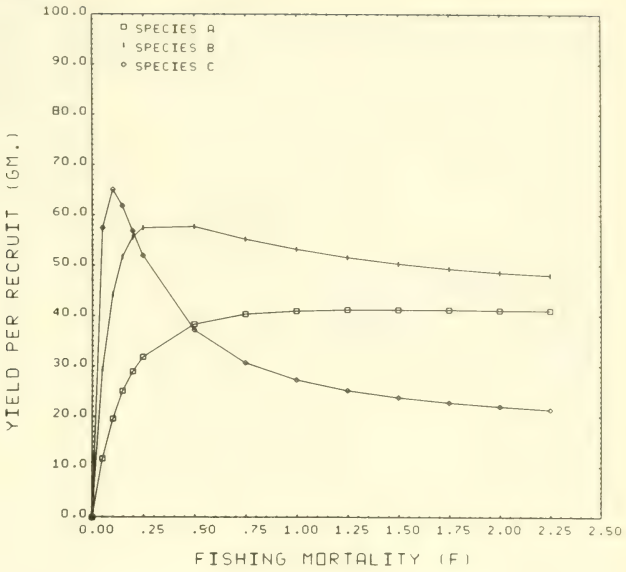


FIGURE 1.—The effect of different levels of fishing mortality with constant age of recruitment (4.2 yr) on yield per recruit of three hypothetical fish species demonstrating the range of r and K selection.

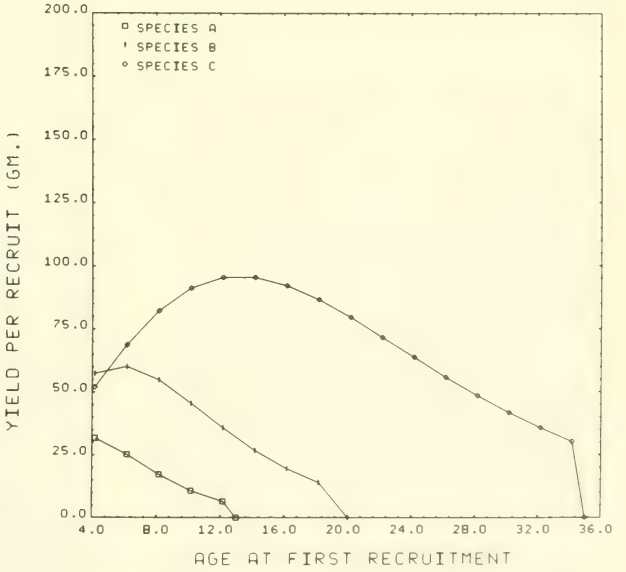


FIGURE 2.—The effect of different mean ages of recruitment at constant fishing mortality ($F = 0.25$) on yield per recruit of three hypothetical fish species demonstrating the range of r and K selection.

selected species than for the r selected species. The K selected species is reduced to levels lower than the maximum sustainable yield by overfishing much more rapidly than the r selected species.

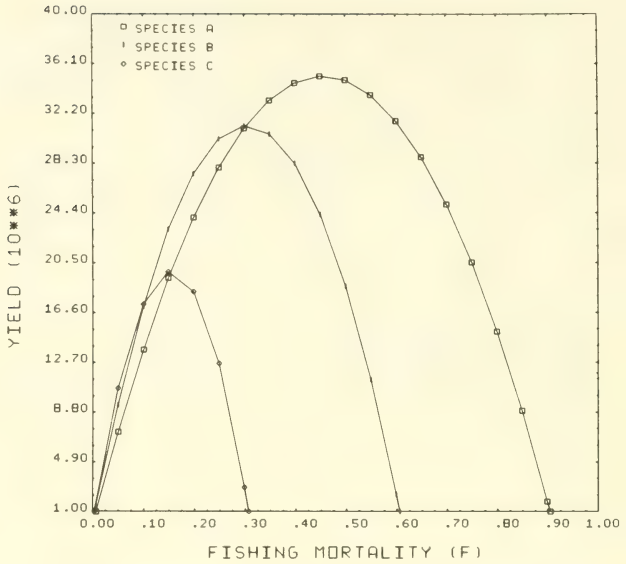


FIGURE 3.—Maximum equilibrium yields ($\times 10^6$ g) from Schaefer surplus production curves as a function of fishing mortality for three hypothetical fish species demonstrating the range of r and K selection.

DISCUSSION

Life history parameters vary in consistent patterns. These patterns are explainable and predictable by the theoretical constructs of r and K selection. This is not a particularly new or unique idea in fisheries biology. Beverton and Holt (1959) investigated a positive relationship between body size and life span and between mortality and growth rates. Cushing (1971) suggested that there is a negative relationship between degree of density dependent regulation and fecundity. Alverson and Carney (1975) have suggested a positive relationship between body size and the time when a cohort maximizes its biomass. In population ecology, similar relationships have been investigated for zooplankton (Allan 1976), plants (Gadgil and Solbrig 1972; MacNaughton 1975), and animals (Smith 1954; Bonner 1965). All these empirical observed trends in life history parameters, along with the trends described here, are consistent with r and K selection.

It is important to reemphasize here the comparative nature of r and K selection. The r and K continuum is a model and as such occurs only in an idealized sense. The idealized r selected species occurs in an ecological vacuum with no density effects and no competition. The idealized K selected species occurs in a completely saturated ecosystem where densities are high compared with carrying capacities and competition for resources is intense. The problem of applying this model to any real situation is not a trivial one. Species are not simply subjected to a single selective pressure, or even to a single set of selective pressures. Because of this, r and K concepts should only be applied in a comparative sense between groups of species that have some degree of functional similarity. No species is r selected or K selected in an absolute sense; it is only relatively more r selected or K selected than some other reference species. This theory will only have value in a situation where the population dynamics of one member of a species group are fairly well understood.

The results of the model analysis give several indications about the reaction to harvesting pressure of species which are more or less r or K selected. Fisheries based on more r selected species will be more productive. They can be fished at younger ages and at higher levels of fishing mortality. Given a minimum population size, these fisheries should also have a quicker recovery from overfishing. Species which are more r

selected are likely to be strongly influenced by physical forces in the environment (Pianka 1974). Relationships of this type, e.g., between anchovies and upwelling, should be important considerations in management plans for these species.

Fisheries based on more *K* selected species will have a high maximum yield per recruit, but there will be fewer fish. Maximum equilibrium yield will occur at later ages of entry into the fishery and at lower levels of fishing mortality. These fisheries would be more susceptible to overfishing and stock depletion. Besides these species' sensitivity to overfishing, more *K* selected species are much more likely to have sophisticated life history mechanisms (Pianka 1974) which would have to be recognized in a management plan. These mechanisms might include parental care systems such as nesting or live births, mating systems, or territoriality. The more *K* selected species are much more likely to have strong interspecific relationships, usually competitive ones. The relationship between competition and harvesting has been dealt with by Larkin (1963) and Tanner (1975). Additional density independent mortality (fishing mortality) increases the advantage for the population with a higher population growth rate (i.e., more *r* selected). Therefore, even low levels of fishing pressure can destabilize a previously stable competitive pair and result in decline of the harvested species. Interestingly, the opposite result is also possible; harvesting pressure can stabilize a previously unstable species pair as Slobodkin (1962) found with experimental populations of hydra.

Fisheries based on more *r* selected species are likely to be of a boom and bust nature. Although in some years catches in these fisheries will be very large, they will be characterized by erratic production levels. The most efficient form of harvesting these fisheries will be fleets which are capable of switching between a number of target species relatively quickly.

Fisheries based on more *K* selected species, in contrast to the boom and bust nature of *r* selected fisheries, will be characterized by relatively stable population sizes and therefore catch levels. Given some initial measure of year class strength, possibly through larval or prerecruitment surveys, the prediction of future catches from that fishery could be made with a fair degree of accuracy. However, once fisheries based on these species become overfished, it would require a long period for the stock to rebuild to levels which can support economical profitable fisheries. An extremely *K* selected species would only be suitable for trophy fisheries.

Fisheries based on *r* and *K* selected species have been discussed in a comparative sense, but predation (in the case of a fishery, human predation) will also have effects on an individual species. The gene pool of any species is going to contain within it some range of variation of both *r* and *K* selected traits. The effects of increasing fishing mortality, which is assumed to be density independent (Cushing 1975), on life history characteristics has been theoretically analyzed by Roughgarden (1971). The general effect is an increase in selective advantage for the *r* selected proportions of the gene pool. This would mean an increase in growth rates, reduced age at first maturity, and greater fecundity at age. These trends will be more conspicuous in species that are relatively more *K* selected. Species that are more strongly *r* selected are likely to have less range of variation in this direction. One example of these effects of predation pressure is a comparison of lake trout, *Salvelinus namaycush*, populations under heavy predation pressure from the freshwater harbor seal, *Phoca vitulina*, to populations in nearby lakes without seals (Power and Gregoire 1978). The lake trout populations which were preyed upon by seals had faster growth rates, small maximum body size, reduced maximum age, lower age at sexual maturity, and greater individual fecundity compared with populations in lakes without seals. Growth and maturation rates of certain seal species have also increased where populations have been reduced by fisheries (Sergeant 1973). These affects can be attributed to changes in selection pressure resulting from sustained harvesting.

In summary, *r* and *K* selection seems to have been an important evolutionary trend on marine fish populations. The basic hypotheses are confirmed by the data presented here. The result of patterns in population parameters which arise from *r* and *K* selection is that different management strategies would be appropriate. The value of this approach is likely to be in initial stages of development of a fishery. As a fishery becomes more developed and more specific information becomes available, a more refined management strategy would become possible.

ACKNOWLEDGMENTS

This paper benefited from readings by M. E. Adams, E. O. Garton, E. S. Hobson, W. H. Lenarz,

and H. Li. Naturally any errors in the paper are the sole responsibility of the author.

LITERATURE CITED

ALANDER, H.
1950. Baltic herring. Ann. Biol. 6:191-192.

ALLAN, J. D.
1976. Life history patterns in zooplankton. Am. Nat. 110:165-180.

ALVERSON, D. L., AND M. J. CARNEY.
1975. A graphic review of the growth and decay of population cohorts. J. Cons. 36:133-143.

ARORA, H. L.
1951. An investigation of the California sand dab, *Citharichthys sordidus* (Girard). Calif. Fish Game 37:3-42.

AYUSHIN, B. N.
1963. Abundance dynamics of herring populations in the seas of the Far East, and reasons for the introduction of fishery regulations. Rapp. P.-V. Réun. Cons. Perm. Int. Explor. Mer 154:262-269.

BARRETT, I., AND G. V. HOWARD.
1961. Studies of the age, growth, sexual maturity and spawning of populations of anchoveta (*Cetengraulis mysticetus*) of the coast of the eastern tropical Pacific Ocean. Inter-Am. Trop. Tuna Comm. Bull. 5:113-165.

BEN-TUVIA, A.
1960. Synopsis of biological data on *Sardinella aurita* of the Mediterranean Sea and other waters. *In* H. Rosa, Jr. and G. Murphy (editors), Proc. World Sci. Meet. Biol. Sardines Relat. Species 2:287-312. FAO, Rome.

BEVERTON, R. J. H.
1963. Maturation, growth and mortality of clupeid and engraulid stocks in relation to fishing. Rapp. P.-V. Réun. Cons. Perm. Int. Explor. Mer 154:44-67.

BEVERTON, R. J. H., AND S. J. HOLT.
1957. On the dynamics of exploited fish populations. Fish. Invest. Minist. Agric., Fish. Food (G.B.), Ser. II, 19, 533 p.
1959. A review of the life spans and mortality rates in nature, and their relation to growth and other physiological characteristics. Ciba Found. Colloq. Ageing 5:142-177.

BLACKBURN, M.
1950. The Tasmanian whitebait, *Lovettia seali* (*Johnson*), and the whitebait fishery. Aust. J. Mar. Freshwater Res. 1:155-198.

BONNER, J. T.
1965. Size and cycle, an essay on the structure of biology. Princeton Univ. Press, Princeton, N.J., 219 p.

BOUGH, P.
1952. La cruissance des poissons mediterrancius. Vie Milieu, Suppl. 2, 2:118-146.

BOWERS, A. B.
1963. Recent changes in the Manx herring fishery. Rapp. P.-V. Réun. Cons. Perm. Int. Explor. Mer 154:220-226.

BURD, A. C.
1962. Growth and recruitment in the herring of the southern North Sea. Fish. Invest. Minist. Agric., Fish. Food (G.B.), Ser. II, 23(5):1-42.

CLARK, F. N., AND J. C. MARR.
1955. Population dynamics of the Pacific sardine. Calif. Ocean. Fish. Invest. Prog. Rep. 1 July 1953 to 31 March 1955, p. 11-48.

CLARK, F. N., AND J. B. PHILLIPS.
1952. The northern anchovy (*Engraulis mordax mordax*) in the California fishery. Calif. Fish Game 38:189-207.

CLAYDEN, A. C.
1972. Simulation of changes in abundance of the cod (*Gadus morhua L.*) and the distribution of fishing in the North Atlantic. Fish. Invest. Minist. Agric., Fish. Food (G.B.), Ser. II, 27(1), 58 p.

CROW, J. F., AND M. KIMURA.
1970. An introduction to population genetics theory. Harper and Row, N.Y., 591 p.

CULLEY, M.
1971. The pilchard, biology and exploitation. Pergamon Press, N.Y., 241 p.

CUSHING, D. H.
1959. On the effect of fishing on the herring of the southern North Sea. J. Cons. 24:283-307.
1961. On the failure of the Plymouth herring fishery. J. Mar. Biol. Assoc. U.K. 41:799-816.
1971. The dependence of recruitment on parent stock in different groups of fishes. J. Cons. 33:340-362.
1975. Marine ecology and fisheries. Camb. Univ. Press, N.Y., 278 p.

DAVIES, D. H.
1958. The South African pilchard (*Sardinops ocellata*), preliminary report on the age composition of the commercial catches, 1950-55. Union S. Afr., Dep. Commer. Indust., Div. Fish. Invest. Rep. 33, 20 p.

DAY, L. R.
1957. Populations of herring in the southern Gulf of St. Lawrence. *In* A. H. Leim, S. N. Tibbo, L. R. Day, L. Lauzier, R. W. Trites, H. B. Hachey, and W. B. Bailey, Report of the Atlantic herring investigation committee, p. 121-137. Fish. Res. Board Can., Bull. 111.

DEASON, H. J., AND R. HILE.
1947. Age and growth of the Kiyi, *Leucichthys kiyi* Koelz, in Lake Michigan. Trans. Am. Fish. Soc. 74:88-142.

DE JAGER, B. V. D.
1960. Synopsis on the biology of the South African pilchard, *Sardinops ocellata* (Pappé). *In* H. Rosa, Jr. and G. Murphy (editors), Proc. World Sci. Meet. Biol. Sardines Relat. Species 2:97-114. FAO, Rome.

DICKIE, L. M., AND F. D. MCCRACKEN.
1955. Isopleth diagrams to predict equilibrium yields of a small flounder fishery. J. Fish. Res. Board Can. 12:187-209.

DRUCKER, B.
1972. Some life history characteristics of coho salmon of the Karluk River system, Kodiak Island, Alaska. Fish. Bull, U.S. 70:79-94.

ELWERTOWSKI, J.
1957. Polish investigations on the sprat from the southern Baltic. Ann. Biol. 12:216.
1958. The sprat in the southern Baltic. Ann. Biol. 13:229-230.
1959. Polish investigations on Baltic sprat in 1957. Ann. Biol. 14:202-203.
1960. Polish investigations on sprat from the southern part of the Central Baltic - 1958. Ann. Biol. 15:192-193.

FAGE, L.
1920. "Engraulidae, Clupeidae". Rep. Danish oceanogr. Exped. Medit., 2(A.9). (Cited in Beverton 1963.)

FAURE, L.
1950. Le sprat de la Baie de Douarnez pêche, biométric et biologie. Rapp. P.-V. Réun. Cons. Perm. Int. Explor. Mer 126:96-102.

FLEMING, A. M.
1960. Age, growth and sexual maturity of cod (*Gadus morhua* L.) in the Newfoundland area, 1947-1950. J. Fish. Res. Board Can. 17:775-809.

FOERSTER, R. E.
1968. The sockeye salmon, *Oncorhynchus nerka*. Fish. Res. Board Can., Bull. 162, 422 p.

FRIDRIKSSON, A.
1950. On the herring of the north coast of Iceland during the summer of 1949. Ann. Biol. 6:162-167.
1951. On the herring and the herring fishery of the north coast of Iceland during the summer of 1950. Ann. Biol. 7:122-125.
1952. The Icelandic north coast herring in 1951. Ann. Biol. 8:136-140.
1953. The Icelandic north coast herring in 1952. Ann. Biol. 9:164-167.
1954. The Icelandic north coast herring in 1953. Ann. Biol. 10:143-147.
1956. The Icelandic north coast herring in 1954. Ann. Biol. 11:114-118.
1957. The Icelandic north coast herring in 1955. Ann. Biol. 12:158-162.
1958. The Icelandic north coast herring in 1956. Ann. Biol. 13:173-176.
1959. The Icelandic north coast herring in 1957. Ann. Biol. 14:149-154.
1960. The Icelandic north coast herring in 1958. Ann. Biol. 15:126-131.
1961. The Icelandic north coast herring in 1959. Ann. Biol. 16:163-167.

FURNESTIN, J.
1945. "Note préliminaire sur l'anchois (*Engraulis encrasicholus* L.) du Golfe de Gascogne". Rev. Trav. Inst. Pêch. Marit. 13:197-209. (Cited in Beverton 1963.)

GADGIL, M., AND W. H. BOSSERT.
1970. Life historical consequences of natural selection. Am. Nat. 104:1-24.

GADGIL, M., AND O. T. SOLBRIG.
1972. The concept of *r*- and *K*-selection: evidence from wild flowers and some theoretical considerations. Am. Nat. 106:14-31.

GILIS, C.
1957. Fall-herring concentrations exploited by the Belgian herring trawlers in 1955. Ann. Biol. 12:204-208.
1958. The Belgian herring fisheries in 1956—1957 (30. July 1956 - 19. January 1957), the North Sea - English Channel. Ann. Biol. 13:205-209.
1959. The Belgian herring fisheries in 1957—1958, the North Sea - English Channel. Ann. Biol. 14:182-188.
1960. The Belgian herring fisheries in 1958—1959. Ann. Biol. 15:176-181.
1961. The Belgian herring fisheries in 1959—1960. Ann. Biol. 16:212-215.

HANAMURA, N.
1953. On the herring resources of Hokkaido and the South Saghalen. Bull. Jpn. Soc. Sci. Fish. 19:283-291.

HANNERZ, L.
1956. Preliminary results of the herring investigations in the Bothnian Sea 1954. Ann. Biol. 11:156-158.

HART, J. L.
1931. The growth of the whitefish *Coregonus clupeaformis* (Mitchell). Contrib. Can. Biol. 6:427-444.
1948. Age and growth rate in the butter sole, *Isopsetta isolepis*. Trans. R. Soc. Can., Ser. 3, Sect. 5, 42:65-72.

HAYASHI, S.
1961. Fishery biology of the Japanese anchovy, *Engraulis japonica* (Houttuyn). Bull. Tokai Reg. Fish. Res. Lab. 31:145-268.

HAYASHI, S., AND K. KONDO.
1957. Growth of the Japanese anchovy—IV. Age determination with use of scales. Bull. Tokai Reg. Fish. Res. Lab. 17:31-64.

HILE, R.
1936. Age and growth of the cisco, *Leucichthys artedi* (Le Sueur), in the lakes of the northeastern highlands, Wisconsin. Bull. U.S. Bur. Fish. 48:211-317.

HILE, R., AND H. J. DEASON.
1934. Growth of the whitefish *Coregonus clupeaformis* (Mitchell), in Trout Lake, northeastern highlands, Wisconsin. Trans. Am. Fish. Soc. 64:231-237.

HODGSON, W. C.
1957. The herring and its fishing. Routledge & Kegan Paul, Lond., 197 p.

HODGSON, W. C., AND I. D. RICHARDSON.
1949. The experiments on the Cornish pilchard fishery in 1947-8. Fish. Invest. Minist. Agric., Fish. Food (G.B.), Ser. II, 27(2), 21 p.

HOLLANDER, M., AND D. A. WOLFE.
1973. Nonparametric statistical methods. Wiley, N.Y., 503 p.

HOLT, S. J.
1962. The application of comparative population studies to fisheries biology—an exploration. *In* E. D. Le Cren and M. W. Holdgate (editors), The exploitation of natural animal populations, p. 51-69. Br. Ecol. Soc. Symp. 2.

JENSEN, A. J. C.
1947. The herring at Bornholm. Ann. Biol. 2:155-158.

KENNEDY, W. A.
1943. The whitefish, *Coregonus clupeaformis* (*Mitchell*), of Lake Opeongo, Algonquin Park, Ontario. Publ. Ont. Fish. Lab. 62:21-66.
1953. Growth, maturity, fecundity and mortality in the relatively unexploited whitefish, *Coregonus clupeaformis*, of Great Slave Lake. J. Fish. Res. Board Can. 10:413-441.
1954. Growth, maturity and mortality in the relatively unexploited lake trout, *Cristivomer namaycush*, of Great Slave Lake. J. Fish. Res. Board Can. 11:827-852.

KETCHEN, K. S.
1964. Preliminary results of studies on growth and mortality of Pacific cod (*Gadus macrocephalus*) in Hecate Strait, British Columbia. J. Fish. Res. Board Can. 21:1051-1067.

KETCHEN, K. S., AND C. R. FORRESTER.
1966. Population dynamics of the petrale sole, *Eopsetta jordani*, in waters off western Canada. Fish. Res. Board Can., Bull. 153, 195 p.

LARKIN, P. A.
1963. Interspecific competition and exploitation. J. Fish Res. Board Can. 20:647-678.

LARRAÑETA, M. G.
1960. Synopsis of biological data on *Sardina pilchardus* of the Mediterranean and adjacent seas. *In* H. Rosa, Jr.

and G. Murphy (editors), Proc. World Sci. Meet. Biol. Sardines Relat. Species 2:137-173. FAO, Rome.

LEA, E.
1919. Age and growth of herring in Canadian waters. *In* J. Hjort (director), Canadian fisheries expedition, 1914-1915, investigations in the Gulf of St. Lawrence and Atlantic waters of Canada, p. 75-164. J. de Labroquerie Tache, Ottawa.

MACARTHUR, R. H., AND E. O. WILSON.
1967. The theory of island biogeography. Princeton Univ. Press, Princeton, N.J., 203 p.

MACKINNON, J. C.
1973. Analysis of energy flow and production in an unexploited marine flatfish population. J. Fish. Res. Board Can. 30:1717-1728.

MACNAUGHTON, S. J.
1975. *r*- and *K*-selection in *Typha*. Am. Nat. 109:251-261.

MENON, M. D.
1950. Bionomics of the poor-cod (*Gadus minutus* L.) in the Plymouth area. J. Mar. Biol. Assoc. U.K. 29:185-240.

MILLER, D. J., A. E. DAUGHERTY, F. E. FELIN, AND J. MACGREGOR.
1955. Age and length composition of the northern anchovy catch off the coast of California in 1952-53 and 1953-54. Calif. Dep. Fish Game, Fish Bull. 101:37-66.

MILLER, D. J., AND R. S. WOLF.
1958. Age and length composition of the northern anchovy catch off the coast of California in 1954-55, 1955-56, and 1956-57. Calif. Dep. Fish Game, Fish Bull. 106:27-72.

MOLANDER, A. R.
1943. Sprat and milieu-conditions. Ann. Biol. 1:165-174.

MOSHER, K. H., AND H. H. ECKLES.
1954. Age determination of Pacific sardines from otoliths. U.S. Fish Wildl. Serv., Res. Rep. 37, 40 p.

MOTODA, S., AND Y. HIRANO.
1963. Review of Japanese herring investigations. Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer 154:249-261.

MURPHY, G. I.
1966. Population biology of the Pacific sardine (*Sardinops caerulea*). Proc. Calif. Acad. Sci., Ser. 4, 34:1-84.

NAIR, R. V.
1960. Synopsis on the biology and fishery of the Indian sardines. *In* H. Rosa, Jr. and G. Murphy (editors), Proc. World Meet. Biol. Sardines Relat. Species 2:329-414.

NIELSEN, J.
1960. Preliminary results of tagging experiments with herring (*Clupea harengus* L.) in Greenland. J. Cons. 26:73-79.

PARRISH, B. B., AND R. E. CRAIG.
1963. The herring of the north-western North Sea, postwar changes in the stock fished by Scottish drifters. Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer 154:139-158.

PHILLIPS, J. B.
1948. Growth of the sardine, *Sardinops caerulea*, 1941-42 through 1946-47. Calif. Div. Fish Game, Fish Bull. 71, 33 p.
1964. Life history studies on ten species of rockfish (genus *Sebastodes*). Calif. Dep. Fish Game, Fish Bull. 126, 70 p.

PIANKA, E. R.
1974. Evolutionary ecology. Harper & Row, N.Y., 356 p.

PINHORN, A. T.
1969. Fishery and biology of Atlantic cod (*Gadus morhua*) off the southwest coast of Newfoundland. J. Fish. Res. Board Can. 26:3133-3164.

POSTEL, E.
1955. Résumé des connaissances acquises sur les clupeides de l'Ouest-Africain. Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer 137:14-16.

POSTUMA, K. H.
1963. The catch per unit effort and mortality rates in the Southern Bight and Channel fisheries. Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer 154:190-197.

POWER, G., AND J. GREGOIRE.
1978. Predation by freshwater seals on the fish community of lower Seal Lake, Quebec. J. Fish. Res. Board Can. 35:844-850.

POWLES, P. M.
1965. Life history and ecology of American plaice (*Hippoglossoides platessoides* F.) in the Magdalen Shallows. J. Fish. Res. Board Can. 22:565-598.
1969. Size changes, mortality, and equilibrium yields in an exploited stock of American plaice (*Hippoglossoides platessoides*). J. Fish. Res. Board Can. 26:1205-1235.

RAITT, D. S.
1939. The rate of mortality of the haddock of the North Sea stock, 1919-1938. Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer 110:65-79.

RICHARDSON, I., G. VAZZOLER, A. DE FARIA, AND M. DE MORAES.
1960. Report on sardine investigations in Brazil. *In* H. Rosa, Jr. and G. Murphy (editors), Proc. World Sci. Meet. Biol. Sardines Relat. Species 3:1051-1079. FAO, Rome.

RICKER, W. E.
1949. Mortality rates in some little-exploited populations of freshwater fishes. Trans. Am. Fish. Soc. 77:114-128.
1958. Handbook of computations for biological statistics of fish populations. Fish. Res. Board Can., Bull. 119, 300 p.
1975. Computation and interpretation of biological statistics of fish populations. Fish. Res. Board Can., Bull. 191, 382 p.

ROBERTSON, J. A.
1938. The sprat and the sprat fishery of England. Fish. Invest. Minist. Agric., Fish. Food (G.B.), Ser. II, 16(2), 103 p.

ROSSIGNOL, M.
1955. Premières observations sur la biologie des Sardinelles dans la région de Pointe-Noire. Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer 137:16-20.

ROUGHGARDEN, J.
1971. Density-dependent natural selection. Ecology 52:453-468.

SCHAFFER, W. M., AND M. D. GADGIL.
1975. Selection for optimal life histories in plants. *In* M. L. Cody and J. M. Diamond (editors), Ecology and evolution of communities, p. 142-157. Harv. Univ. Press, Camb., Mass.

SERGEANT, D. E.
1973. Environment and reproduction in seals. J. Reprod. Fertil. Suppl. 19:555-561.

SHAPOVALOV, L., AND A. C. TAFT.
1954. The life histories of the steelhead rainbow trout (*Salmo gairdneri gairdneri*) and silver salmon (*Oncorhynchus kisutch*) with special reference to Waddell Creek, California, and recommendations regarding their management. Calif. Dep. Fish Game, Fish Bull. 98, 375 p.

SILLIMAN, R. P.
1943. Studies on the Pacific pilchard or sardine (*Sardinops caerulea*). 5.—A method of computing mortalities and re-

placements. U.S. Fish Wildl. Serv., Spec. Sci. Rep. 24, 10 p.

SLOBODKIN, L. B.
1962. Growth and regulation of animal populations. Holt, Rinehart and Winston, N.Y., 184 p.

SMITH, F. E.
1954. Quantitative aspects of population growth. *In* E. J. Boell (editor), Dynamics of growth process, p. 277-294. Princeton Univ. Press, Princeton, N.J.

SMITH, W. C.
1957. Gonad condition, age and size of Manx herrings, 1945-53, and comparison with earlier years. Annu. Rep. Mar. Biol. Stn. Pt. Erin. 69:21-28.

SOUTHWOOD, T. R. E., AND H. N. COMINS.
1976. A synoptic population model. J. Anim. Ecol. 45:949-965.

SOUTHWOOD, T. R. E., R. M. MAY, M. P. HASSELL, AND G. R. CONWAY.
1974. Ecological strategies and population parameters. Am. Nat. 108:791-804.

SUND, O.
1943a. The age-composition of the Norwegian spawn herring observed during 36 years. Ann. Biol. 1:45-49.
1943b. The size of the Norwegian spawn herring. Ann. Biol. 1:50-51.

TANAKA, S.
1960. Studies on the dynamics and the management of fish populations. [In Jpn., Engl. summ.] Bull. Tokai Reg. Fish. Res. Lab. 28:1-200.

TANNER, J. T.
1975. The stability and the intrinsic growth rates of prey and predator populations. Ecology 56:855-867.

TAYLOR, C. C.
1958. Cod growth and temperature. J. Cons. 23:366-370.

TESTER, A. L.
1955. Estimation of recruitment and natural mortality rate from age-composition and catch data in British Columbia herring populations. J. Fish. Res. Board Can. 12:649-681.

TIBBO, S. N.
1956. Populations of herring (*Clupea harengus* L.) in Newfoundland waters. J. Fish. Res. Board Can. 13:449-466.
1957a. Herring of the Chaleur Bay area. *In* A. H. Leim, S. N. Tibbo, L. R. Day, L. Lauzier, R. W. Trites, H. B. Hachey, and W. B. Bailey, Report of the Atlantic herring investigation committee, p. 85-102. Fish. Res. Board Can., Bull. 111.
1957b. Herring populations on the south and west coasts of Newfoundland. *In* A. H. Leim, S. N. Tibbo, L. R. Day, L. Lauzier, R. W. Trites, H. B. Hachey, and W. B. Bailey, Report of the Atlantic herring investigation committee, p. 153-164. Fish. Res. Board Can., Bull. 111.

TOKAI REGIONAL FISHERIES RESEARCH LABORATORY.
1960. Synopsis on the biology of *Sardinops melanosticta* (Temminck and Schlegel). *In* H. Rosa, Jr. and G. Murphy (editors), Proc. World Sci. Meet. Biol. Sardines Relat. Species 2:213-244. FAO, Rome.

VAN CLEVE, R., AND D. E. BEVAN.
1973. Evaluation of causes for the decline of the Karluk sockeye salmon runs and recommendations for rehabilitation. Fish. Bull., U.S. 71:627-649.

WATANABE, K.
1958. Growth of the anchovy in the Japan Sea. Annu. Rep. Jpn. Sea Fish. Res. Lab. 4:147-152.

APPENDIX I: LITERATURE CITATIONS FOR POPULATION PARAMETERS BY SPECIES

Herring and Anchovies, Families Clupeidae and Engraulidae

Clupea harengus—Lea 1919; Sund 1943a, b; Jensen 1947; Fridriksson 1950, 1951-61; Alander 1950; Tibbo 1956, 1957a, b; Hannerz 1956; Gilis 1957-61; Smith 1957; Day 1957; Cushing 1959; Nielsen 1960; Burd 1962; Parrish and Craig 1963; Postuma 1963; Bowers 1963.

C. pallasii—Hanamura 1953; Tester 1955; Ricker 1958; Tanaka 1960; Ayushin 1963; Motoda and Hirano 1963.

Sprattus sprattus—Robertson 1938; Molander 1943; Faure 1950; Elwertowski 1957-60.

Sardinops caerulea—Silliman 1943; Phillips 1948; Mosher and Eckles 1954; Clark and Marr 1955; Murphy 1966; Culley 1971.

S. melanosticta—Tanaka 1960; Tokai Regional Fisheries Research Laboratory 1960.

S. neopilchardus—Blackburn 1950.

S. ocellata—Davies 1958; De Jager 1960; Culley 1971.

Sardina pilchardus—Hodgson and Richardson 1949; Bough 1952; Hodgson 1957; Larrañeta 1960; Cushing 1961; Culley 1971.

Sardinella aurita—Postel 1955; Rossignol 1955; Richardson et al. 1960; Ben-Tuvia 1960; Beverton 1963.

S. longiceps—Nair 1960.

Engraulis encrasicholus—Fage 1920; Furnestin 1945.

E. japonicus—Hayashi and Kondo 1957; Watanabe 1958; Tanaka 1960; Hayashi 1961.

E. mordax mordax—Clark and Phillips 1952; Miller et al. 1955; Miller and Wolf 1958; Culley 1971.

Cetengraulis mysticetus—Barrett and Howard 1961.

Salmons, Family Salmonidae

Coregonus clupeaformis—Hart 1931; Hile and Deason 1934; Kennedy 1943, 1953; Ricker 1949.
Cristivomer namaycush—Kennedy 1954.
Leucichthys artedii—Hile 1936.
L. kiyi—Deason and Hile 1947.
Oncorhynchus kisutch—Shapovalov and Taft 1954; Drucker 1972.
O. nerka—Foerster 1968; Van Cleve and Bevan 1973.

Cods, Family Gadidae

Boreogadus saida—Beverton and Holt 1959.
Gadus callarias—Beverton and Holt 1957; Taylor 1958.
G. macrocephalus—Ketchen 1964.
G. minutus—Menon 1950.
G. morhua—Fleming 1960; Pinhorn 1969; Clayden 1972.
G. virens—Beverton and Holt 1959.
Melanogrammus aeglefinus—Raitt 1939; Beverton and Holt 1957.
Merluccius merluccius—Beverton and Holt 1959.

Rockfishes, Family Scorpaenidae, Genus *Sebastodes*

Sebastodes crameri—Phillips 1964.
S. diploproa—Phillips 1964.
S. entomelas—Phillips 1964.
S. flavidus—Phillips 1964.
S. goodei—Phillips 1964.
S. jordani—Phillips 1964.
S. miniatus—Phillips 1964.
S. paucispinis—Phillips 1964.
S. pinniger—Phillips 1964.
S. saxicola—Phillips 1964.

Flatfishes, Order Pleuronectiformes

Citharichthys sordidus—Arora 1951.
Eopsetta jordani—Ketchen and Forrester 1966.
Hippoglossus platessoides—Powles 1965, 1969; MacKinnon 1973.
H. vulgaris—Beverton and Holt 1959.
Isopsetta isolepis—Hart 1948.
Pleuronectes platessa—Beverton and Holt 1959.
Pseudopleuronectes americanus—Dickie and McCracken 1955.
Solea vulgaris—Beverton and Holt 1957.

SPECIES OF *MUNIDOPSIS* (CRUSTACEA, GALATHEIDAE) OCCURRING OFF OREGON AND IN ADJACENT WATERS

JULIE W. AMBLER[1]

ABSTRACT

Twelve species of *Munidopsis* (Decapoda: Crustacea: Galatheidae) were collected from the continental slope, Cascadia Basin, and Tufts Abyssal Plain off Oregon and in adjacent waters. Three new species are described: *Munidopsis cascadia, M. tuftsi,* and *M. yaquinensis*. One specimen, *Munidopsis* sp., closely related to *M. bairdii*, is described but unnamed, pending capture of more specimens. *Munidopsis chacei* is synonymized with *M. bairdii* and *M. geyeri* is synonymized with *M. subsquamosa*. The ranges of seven previously described species are now extended to Oregon and Washington: *M. aries, M. bairdii, M. beringana, M. ciliata, M. latirostris, M. subsquamosa,* and *M. verrucosus*. The 12 species occurred between 950 and 4,194 m; 3 species were found on the continental slope (950-2,189 m); 9 species were found on Cascadia Basin (1,900-3,025 m); and 3 species were found on Tufts Plain (3,390-4,194 m). Species composition on Cascadia Basin differed from east to west. The highest densities (number of specimens per trawl) occurred at the base of the continental slope and 40 miles farther west. One species, *M. latirostris*, contributed 73.0% of the total number of specimens, and three other species (*M. bairdii, M. ciliata*, and *M. subsquamosa*) contributed an additional 20.2%. The species collected also occur in the Atlantic (*M. bairdii, M. aries*), tropical Pacific and Indian (*M. ciliata*), tropical Pacific (*M. latirostris*), Arctic (*M. beringana*), southern temperate Pacific (*M. verrucosus*), or are cosmopolitan (*M. subsquamosa*), or are endemic on Cascadia Basin (*M. cascadia, M. yaquinensis*), and on Tufts Plain (*M. tuftsi*).

Species of *Munidopsis* are found from intertidal waters to the abyssal plains of the deep sea. *Munidopsis polymorpha* is found in saltwater lakes in caverns connected to the sea in the Canary Islands (Dinkins 1969). *Munidopsis crassa*, the deepest known species, was found at 4,700 m in the Bay of Biscay (Sivertson and Holthuis 1956). Recently, an unidentified *Munidopsis* sp. has been found near submarine hot springs near the Galapagos (Corliss and Ballard 1977). In general, the genus is found in the deep sea with about half of the known species occurring deeper than 800 m (Doflein and Balss 1913).

In the eastern Pacific Ocean, the first *Munidopsis* species were collected off Chile by the *Challenger* (Henderson 1888) and in the eastern tropical Pacific by the *Albatross* (Faxon 1895). Benedict (1902) described additional new species collected by the *Albatross* off southern California and the Galapagos, and in the Bering Sea. Since then, Bahamonde (1964) and Khodkina (1973) have found new species off Chile, and Pequegnat and Pequegnat (1973) described a new species off Baja California and Costa Rica from the *Albatross* and *Galathea* collections. Little work has been done on *Munidopsis* occurring off the west coast of the United States. Schmitt (1921), in a key to *Munidopsis* species found off California, included *M. verrilli, M. hystrix, M. aspera*, and *M. quadrata*. Haig (1956) modified this key to include *M. depressa*.

This paper discusses the taxonomy and distribution of 12 *Munidopsis* species collected mainly off Oregon from 950 to 4,194 m. These depths include the lower slope and the abyssal plains of Cascadia Basin and Tufts Plain (Figure 1). Among species found off Oregon, only *M. quadrata* has previously been collected from the west coast of the United States. Three new species are described: *M. cascadia, M. tuftsi,* and *M. yaquinensis*. One species, *Munidopsis* sp., is described but left unnamed until more specimens become available to elucidate its relationship to *M. bairdii*. The ranges of seven previously described species are extended to Oregon: *M. bairdii, M. beringana, M. ciliata, M. aries, M. verrucosus, M. latirostris,* and *M. subsquamosa*.

METHODS

A total of 803 specimens were collected from 146

[1]School of Oceanography, Oregon State University, Corvallis, Oreg.; present address: Department of Oceanography, Texas A&M University, College Station, TX 77843.

Manuscript accepted August 1979.
FISHERY BULLETIN: VOL. 78, NO. 1, 1980.

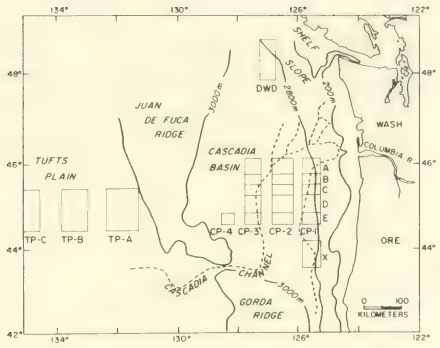


FIGURE 1.—Stations sampled in Cascadia Basin and Tufts Plain, off Oregon and Washington.

benthic otter trawls (OTB, OT) and beam trawls (BMT) during 13 yr of sampling by Andrew G. Carey, Jr., School of Oceanography, Oregon State University. On Cascadia Basin, samples were collected on three north-south lines ranging from the CP-1 line (Figure 1) at the base of the continental slope to the CP-3 line 80 mi farther offshore. The base of the continental slope varies from 1,900 m on the Astoria Fan at CP-1-A to 2,816 m at CP-1-E. At the base of the continental slope farther south, between lat. 43° and 44° N, a small trench occurs in which depths reach 3,000 m. Stations become deeper both to the south and to the west in Cascadia Basin. One sample was taken from Gorda Ridge off California, south of Cascadia Basin. Ten tows were made in northern Cascadia Basin on Nitinat Fan off Washington, during a study of deepwater dumpsites (Carey et al. 1973). Three areas (TP-C, TP-B, TP-A) were sampled on Tufts Plain. Station abbreviations are as follows: NAD = Newport hydrographic line, mainly slope stations; CP = Cascadia Basin, off Oregon; TP = Tufts Plain; and DWD = Deepwater dumpsite, northern Cascadia Basin, off Washington.

The beam trawl is a semiquantitative sampler (Carey and Heyamoto 1972), with a rigid frame of steel skids connected by a 3 m aluminum pipe, with a collecting net of 4.1 cm stretch mesh lined with 1.3 cm mesh net. The otter trawl is a 7 m semiballoon Gulf of Mexico shrimp trawl with 4.1 cm stretch mesh with a 1.3 cm mesh liner. Samples were preserved at sea in 10% formaldehyde and sorted in the laboratory.

The specimens were examined through a dissecting microscope and measured with vernier calipers usually to the nearest millimeter. The following measurements were used (Figure 2):

Carapace length (CL) = tip of rostrum to middle of posterior margin of carapace.
Anterior width of carapace = width between anterolateral spines.
Posterior width of carapace = width at posterior margin of carapace.
Rostrum length = tip of rostrum to rostrum base, which lies on an imaginary line between the bases of the ocular peduncles.
Cheliped length = tip of chela to articulation between ischium and sternum.
Chela length = tip of chela to articulation between chela and carpus, on the ventral side.
Eyespine length = tip of eyespine to proximal end of cornea.

Incomplete synonymies are given for each species. References include original description, first redescription if the original description was very short, first figure, and all synonyms.

The specimens from Oregon State University (OSU) were compared with those borrowed from the U.S. National Museum (USNM), the Museum of Comparative Zoology at Harvard (MCZ), and from Texas A&M University (TAMU). Specimens of each species are cataloged in the Oregon State University Benthic Invertebrate Museum (OSUBI). The holotypes and a few paratypes of the new species were deposited at the U.S. National Museum.

MUNIDOPSIS WHITEAVES 1874

Munidopsis Whiteaves 1874:212 (original description); Smith 1885:493 (synonomy with *Galacantha*); Milne-Edwards and Bouvier 1894:271, 1897:63 (redescriptions); Faxon 1895:81-83 (synonomy with *Orophorhynchus, Elasmonotus, Galathodes,* and *Anoplonotus*); Chace 1942:69 (synonomy with *Galacantha*).

Galathodes Milne-Edwards 1880:53 (original description); Milne-Edwards and Bouvier 1894:276, 1897:94 (redescriptions).

Orophorhynchus Milne-Edwards 1880:58 (original description); Milne-Edwards and Bouvier 1894:283, 1897:110 (redescriptions).

Elasmonotus Milne-Edwards 1880:60 (original description); Milne-Edwards and Bouvier 1894:279, 1897:98 (redescriptions); Henderson 1888:165 (synonomy with *Galathopsis*).

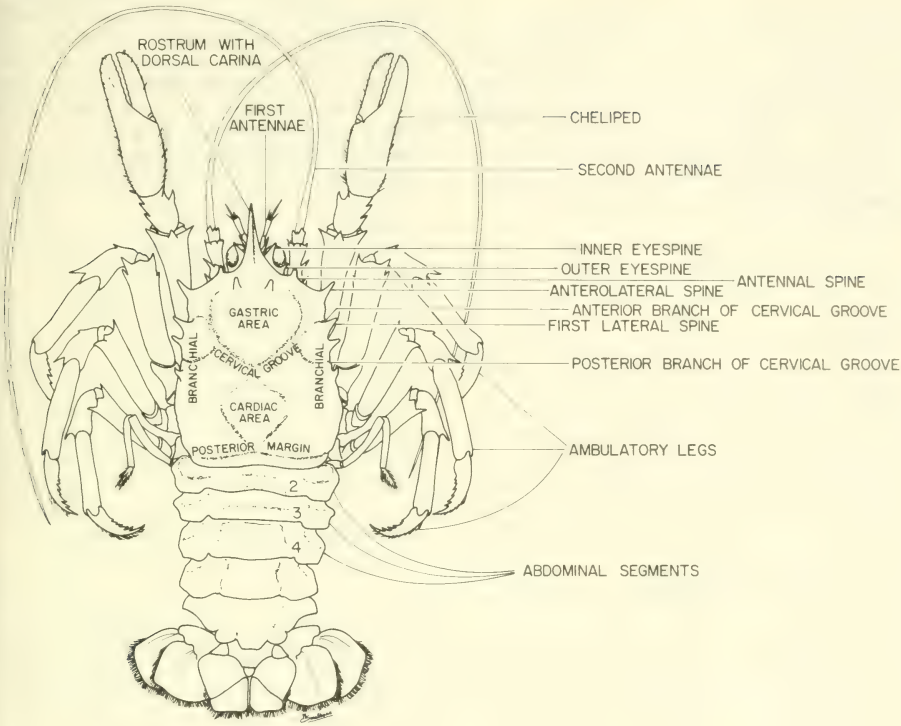


FIGURE 2.—Generalized drawing of the genus *Munidopsis*.

Anoplonotus Smith 1883:50 (original description).
Galathopsis Henderson 1885:417 (original description).
Galacantha Milne-Edwards 1880:52 (original description); Henderson 1888:166 (redescription, argues for separate genus); Milne-Edwards and Bouvier 1894:268, 1897:55 (redescriptions).

Diagnosis.—Integument heavily calcified; carapace longer than wide, covered with spines, sometimes with setae, and with rugae often in transverse rows; dorsal surface of carapace with well-defined cardiac and gastric areas, gastric area separated from branchial area by cervical groove; anterolateral borders of carapace usually spinose or dentate but occasionally entire; anterior border of carapace sometimes with small supra-antennal spine or tooth, never with a long supraorbital spine; eyes small, unfaceted, and devoid of pigment; ocular peduncle sometimes extended beyond cornea as a spine (eyespine); rostrum well developed, triangular or spatulate; antennular peduncle with short flagellum; antennal peduncle four jointed, usually with long flagellum; chelipeds either longer or shorter than next three ambulatory legs, epipodite present sometimes on chelipeds and occasionally on ambulatory legs; moderate number of large eggs, a few millimeters in diameter.

The genus *Munidopsis* (including *Galacantha*) has about 140 species with 112 of them covered in checklists by Doflein and Balss (1913) and 101 in a checklist by Benedict (1902). The genus has been divided into five groups called either genera, subgenera, or groups (Henderson 1888; Milne-Edwards and Bouvier 1894; Alcock 1901; Tirmizi 1966). Faxon (1895) and Chace (1942) recommended a single genus *Munidopsis* because many

species show characteristics intermediate between groups.

Several extensive keys exist. Benedict's (1902) key describes all specimens in the U.S. National Museum collection at that time. Chace (1942) wrote a key to the western Atlantic species, which has been updated by Pequegnat and Pequegnat (1970, 1971). Other extensive keys were constructed by Milne-Edwards and Bouvier (1894) and Alcock (1901).

Characteristics of Taxonomic Importance for Species

Although the antennular peduncle, antennal peduncle, and merus of the third maxilliped are usually drawn for new species, these characters are rarely used to identify species.

Carapace. Presence, absence, and number of spines on the anterior, lateral, and posterior margins and on the dorsal surface of the carapace. Presence of the antennal spine variable among specimens of the same species. The basic type of ornamentation (ridges, tubercles, crenulations, spines, setae) on the dorsal surface. Slight differences in ornamentation, size, and spacing found on specimens from different geographic locations are considered varietal differences.

Rostrum. The general shape: triangular or rounded. Lateral margins armed with spines or unarmed.

Eyespines. Presence or absence; length in relation to cornea; sharp or blunt.

Chelipeds. Length compared with carapace length; ornamentation, especially spines on segments.

Walking legs. Not as important as chelipeds. General ornamentation.

Epipodites on chelipeds and legs. Presence or absence.

Abdomen. Presence or absence of spines on dorsal surface.

Key to Species of *Munidopsis* off Oregon and Washington

1a.	No epipods on chelipeds	2
1b.	Epipods present on chelipeds	5
2a.	Eyespines absent; one large spine on second, third, and fourth abdominal segments; frontal and lateral margin of carapace forms a right angle	*quadrata*
2b.	Eyespines present; abdomen unarmed; spine or tooth present at anterolateral corner of carapace	3
3a.	Wide, triangular rostrum; posterior margin of carapace unarmed	*aries*
3b.	Narrow rostrum with or without lateral spines; posterior margin of carapace armed with 1 to 10 spines	4
4a.	Rostrum with 2-6 lateral spines, posterior margin of carapace armed with 3-10 (usually 4-6) spines; chela with 2 inner spines	*bairdii*
4b.	Rostrum with no lateral spines; posterior margin of carapace armed with one spine; chela without two inner spines	sp.
5a.	Eyestalks extend beyond eye as definite, sharp spines	6
5b.	Eyestalks extend beyond eye as blunt processes	11
6a.	Two eyespines present, a longer inner spine and a short outer spine	*ciliata*
6b.	Only inner eyespine present	7
7a.	Rostrum wide, not triangular, with dorsal carina, rounded at end	*yaquinensis*
7b.	Rostrum triangular, with dorsal carina and pointed at end	8
8a.	Carapace and legs covered densely with setae; lateral margins of carapace without spines	*cascadia*
8b.	Carapace and legs not covered densely with setae; spines on lateral margins of carapace	9

9a. Thin, unarmed rostrum strongly upturned ..... *beringana*
9b. Triangular rostrum armed with spines or teeth, not upturned 10

10a. Rostrum armed laterally with two to four small spines; carapace covered with crenulated (margin cut into rounded scallops) tubercles; eyespines long, anterolateral spine about same size as first lateral spine ..... *tuftsi*
10b. Rostrum armed laterally with minute teeth; carapace covered with semicircular scalelike tubercles with long setae; eyespines short; anterolateral spine larger than first lateral spine ..... *subsquamosa*

11a. Rostrum triangular without dorsal carina; large spine on second, third, and fourth abdominal segments ..... *verrucosus*
11b. Rostrum wide at base, nearly parallel to eyestalks, with dorsal carina; abdomen with no large spines ..... *latirostris*

Munidopsis quadrata Faxon 1893

Munidopsis quadrata Faxon 1893:1888 (original description); Faxon 1895:97 (redescription), pl. 23, fig. 1, 1e.
Elasmonotus quadratus Milne-Edwards and Bouvier 1894:281-282 (under discussion of genus *Elasmonotus*, key to *Elasmonotus*).

Material.—OSUBI 00170, gravid female, 11 mm CL, stn NAD 11, 44°39.0′ N, 124°59.9′ W, BMT 312, 950 m; OSUBI 00171, male, 13 mm CL, stn Waldpt., 44°21.7′ N, 125°07.9′ W, OT 27, 1,000 m; OSUBI 00182, gravid female, 12 mm CL, male, 11 mm CL, stn NAD 12, 44°38.8′ N, 125°09.1′ W, OTB 360, 1,170 m; OSUBI 01580, 2 specimens, stn DWD 5, 48°38.1′ N, 126°58.1′ W, BMT 9, 2,189 m.

Distribution.—The range of *Munidopsis quadrata* extends from off Destruction Island, Wash., to Tres Marias Islands, Mexico, at depths usually between 620 and 1,571 m; it has also been found at 86 and 110 m, off Wilmington, Calif., and Los Coronados Islands, respectively (Rathbun 1904). These shallow records (86 and 110 m) seem unlikely when compared with the usual depth range of 620-1,571 m, although other species of *Munidopsis* do occur on the Continental Shelf. *Munidopsis quadrata* occurs on the continental slope off Oregon and on the Nitinat Fan off Washington at 950-2,189 m, which extends the known depth range.

Munidopsis aries (Milne-Edwards 1880)

Orophorhynchus aries Milne-Edwards 1880:58 (original description); Milne-Edwards and Bouvier 1897:111-113 (redescription), pl. 9.
Munidopsis aries. Benedict 1902:316 (genus changed to *Munidopsis*).

Material.—USNM 171346, female, 43 mm CL, stn CP-2-E, 44°38.4′ N, 126°42.0′ W, BMT 270, 2,850 m; OSUBI 00169, female, 29 mm CL, stn CP-3-E Channel, 44°44.4′ N, 127°22.1′ W, BMT 359, 3,025 m. The holotype was not examined.

Remarks.—This species is known from only three specimens—the type and two Oregon specimens (Table 1). *Munidopsis sundi* and *M. albatrossae*, both giant species, are most similar to *M. aries* in shape and ornamentation of the carapace.

The description of *M. aries* (Milne-Edwards and Bouvier 1897) fits the Oregon specimens except for the chelipeds. In the Oregon specimens, the merus of the cheliped has four small spines at the anterior border and a row of small spines along the dorsal ridge; the carpus has four or five small spines on the dorsal surface with two or three of these at the anterior border. Milne-Edwards and Bouvier (1897) described two denticles at the anterior border of the merus and the carpus. They did not describe the inner margin of the merus of the third maxilliped. In the Oregon specimens three

TABLE 1.—Morphometry of *Munidopsis aries*. Data on holotype from Milne-Edwards and Bouvier (1897).

Measurement (mm)	Holotype	USNM 171346	OSUBI 00169
Carapace length	20	43	29
Rostrum length	5.1	12	8
Anterior carapace width	9.7	18	14
Posterior carapace width	10.5	26	18
Width at widest part of carapace	14	29	19
Cheliped length	18	37	24
Rostrum length/carapace length	0.26	0.28	0.28
Cheliped length/carapace length	0.90	0.86	0.83

small spines occur along the posterior half of this inner margin.

Distribution.—*Munidopsis aries* appears to be a rare, deepwater species. The type is from near Bequia in the Caribbean Sea (lat. 13° N, long. 61.1° W) at 2,912 m. The Oregon specimens were collected at 2,850 m in Cascadia Basin and at 3,025 m in Cascadia Channel.

Munidopsis bairdii (Smith 1884)

Galacantha bairdii Smith 1884:356 (original description).
Munidopsis bairdii. Smith 1886:649 (redescription) pl. 5, fig. 2.
Munidopsis chacei. Kensley 1968:288 (original description) fig. 1.

Material.—Holotype, USNM 5717, female, 45 mm CL, *Albatross* stn 2106, 37°41.3′ N, 73°3.3′ W, 2,740 m; USNM 10801, male, *Albatross* stn 2573, 40°34.3′ N, 66°09′ W, 3,188 m; USNM 171344, male, 48 mm CL, male, 41 mm CL, stn CP-2-B, 45°34.5′ N, 126°18.5′ W, BMT 156, 2,661 m; OSUBI 00193, female, 28+ mm CL, stn CP-2-E, 44°43.4′ N, 126°27.5′ W, OTB 90, 2,772 m; OSUBI 00192, 6 specimens, stn CP-2-C, 45°20.8′ N, 126°37.7′ W, BMT 264, 2,750 m; OSUBI 00194, female, 22 m CL, stn CP-2-D, 44°53.7′ N, 126°33.4′ W, BMT 162, 2,774 m; 51 uncataloged specimens, smallest ovigerous female 43 mm CL.

Remarks.—The characteristics of *Munidopsis chacei* Kensley, are within the range of variation of *M. bairdii* and, therefore, *M. chacei* is here considered a synonym of *M. bairdii*. As noted by Kensley (1968), *M. chacei* and *M. bairdii* differ in the number of spines of the gastric and cardiac areas and on the posterior margin, and the ratio of dactyl to propodal length of the ambulatory legs. However, the range of variation of these characteristics in our specimens of *M. bairdii* includes those observed for *M. chacei* (Table 2).

Munidopsis columbiana Pequegnat and Pequegnat is a closely related species, with the following differentiating characteristics: antennal spines present in *M. columbiana*, absent in *M. bairdii*; abdominal segments with spines in *M. columbiana*, absent in *M. bairdii*; and inner margin of merus of third maxilliped with five to eight teeth in *M. columbiana*, three teeth in *M. bairdii*, and two to four teeth in our specimens.

TABLE 2.—Selected spine counts of *Munidopsis chacei* and *M. bairdii* from their type descriptions, compared with data from 46 Oregon specimens.

Item	Gastric area	Cardiac area	Posterior margin
M. chacei:			
Kensley (1968)	5	4	4
M. bairdii:			
USNM 5717	6	3	10
USNM 10801	5	3	4
Faxon (1895)	4	1	5
Oregon specimens	3-5	2-4	4-6

Pequegnat and Pequegnat (1971) mention two other characteristics, but these do not separate the two species. In their key, the presence of more than seven spines on the carapace separates *M. columbiana* from *M. bairdii*. In the Oregon specimens, the number of spines on the carapace ranges from 5 to 11. The number of lateral spines on the rostrum is not a distinguishing characteristic. *Munidopsis columbiana* can have from two to six lateral spines, but usually has four. The type of *M. bairdii* has six lateral spines. In the Oregon specimens the number of spines ranges from two to six, but usually is four.

Distribution.—*Munidopsis bairdii* occurs at depths of 2,377-2,940 m in Cascadia Basin. It has been previously collected in both the Atlantic and Pacific Oceans: Cape Sable to Cape May (Smith 1886); Cape Hatteras to Nantucket (Smith 1884); off Panama (Faxon 1895); and off the west coast of the Cape Peninsula or Cape Point, South Africa (Kensley 1968).

Munidopsis sp. (Figure 3)

Munidopsis sp. USNM 171345, male, 20 mm CL, stn NAD 17, 44°31.2′ N, 125°15.5′ W, OT 23, 1,829 m.

Remarks.—*Munidopsis* sp. closely resembles *Munidopsis bairdii*, but is distinctly different in some characters. More specimens are needed to verify species status. The form differs from *M. bairdii* in having no lateral spines on the rostrum, a shorter rostrum, only one spine on the posterior margin, rugae on carapace much less pronounced, hairs on carapace thicker, shorter eyespines extending just beyond the cornea, and the chelae not armed with two inner spines. However, *Munidopsis* sp. has four spines on the gastric area and three on the cardiac area, which are within the range found for *M. bairdii*.

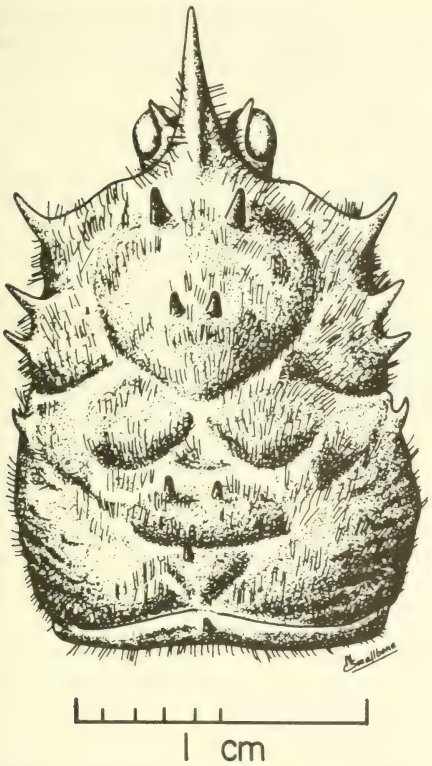


FIGURE 3.—*Munidopsis* sp. (similar to *Munidopsis bairdii*) USNM 171345, dorsal view of carapace.

Distribution.—*Munidopsis* sp. has only been collected from the lower continental slope at 1,829 m, which does not overlap with the depth range of *M. bairdii* (2,377-2,940 m).

Munidopsis ciliata Wood-Mason 1891

Munidopsis brevimana Henderson 1885:414 (original description); Henderson 1888:154 (redescription), pl. 17, fig. 1, 2.

Munidopsis ciliata Wood-Mason 1891:200 (original description); Faxon 1895:84 (synonymy with *M. brevimana*, comparison with *M. nitida*); Faxon 1895:81-82 (*M. ciliata* because genus synonomy caused prior usage of *M. brevimana*), pl. 18, fig. 3.

Material.—MCZ 4540, female, 27 mm CL, *Albatross* stn 3392, 7°5.5′ N, 79°40.0′ W, 2,324 m; MCZ 4541, male, 19 mm CL, *Albatross* stn 3393, 7°15.0′ N, 79°37.0′ W, 1,867 m; USNM 171342, female, 13 mm CL, stn CP-1-A, 45°55.3′ N, 125°36.1′ W, BMT 194, 2,030 m; USNM 171343, 13 specimens, stn CP-2-A, 45°52.5′ N, 126°40.8′ W, BMT 154, 2,666 m; OSUBI 00188, male, 15 mm CL, stn CP-1-E, 44°39.8′ N, 125°36.4′ W, BMT 184, 2,875 m; OSUBI 00189, 33 specimens, stn CP-2-D, 44°53.7′ N, 126°33.4′ W, BMT 162, 2,774 m; OSUBI 01581, females, 16 mm CL, stn CP-2-A, 45°48.3′ N, 126°28.2′ W, BMT 158, 2,651 m; OSUBI 01578, female, 12 mm CL, stn CP-2-C, 45°18.6′ N, 126°31.5′ W, BMT 265, 2,750 m.

Comparative material.—*Munidopsis nitida*: USNM 21287, female, 21 mm CL, *Albatross* stn 2140, 17°36.2′ N, 76°46.1′ W, 1,768 m. *Munidopsis verrilli*: Holotype, USNM 20556, female, 22 mm CL, *Albatross* stn 2923, 32°40.5′ N, 117°31.5′ W, 1,504 m.

Remarks.—The Oregon specimens differ from the *Albatross* specimens by the shorter, stouter spines on the carapace and legs; shorter setae covering the carapace and legs; rostrum with a narrower base; and no extra spine between the anterolateral and antennal spines, as sometimes occurs in the *Albatross* specimens (Figure 4). A small ventral spine occurs behind the large inner eye-spine on the Oregon specimens. Carapace sculpturing is similar in all specimens. I conclude that the observed differences are racial or varietal rather than specific. All specimens are from the Indian and Pacific Oceans.

Munidopsis ciliata is closely related to *M. nitida* Milne-Edwards, but has a more sculptured carapace. Faxon (1895) suggested the differences may be racial or varietal rather than specific. *Munidopsis nitida* has only been found in the Atlantic Ocean (Milne-Edwards 1880; Pequegnat and Pequegnat 1970). Because of the distinct differences in carapace sculpture, I consider *M. ciliata* and *M. nitida* to be separate species.

Both *M. ciliata* and *M. nitida* are closely related to *M. verrilli* Benedict, but differ in that *M. verrilli* has no epipods on the chelipeds or walking legs, whereas *M. ciliata* and *M. nitida* have epipods on only the chelipeds; *M. verrilli* has two spines on the crest of the chela and two spines on the inner edge of the merus of the cheliped, whereas *M. ciliata* and *M. nitida* do not; *M. verrilli* does not

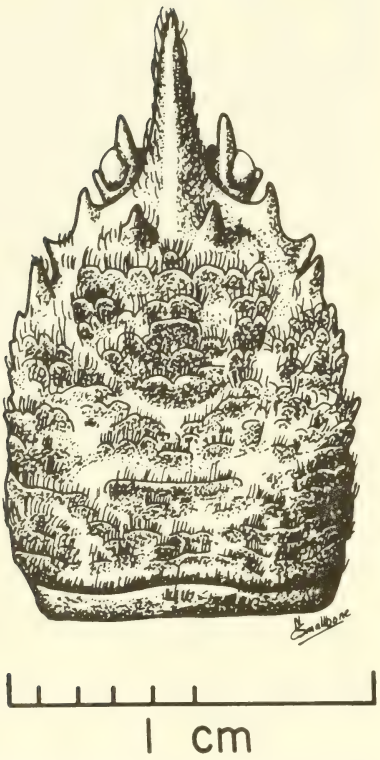


FIGURE 4.—*Munidopsis ciliata*, dorsal view of carapace.

have an inner spine on the third segment of the antennae, which is present in *M. ciliata* and *M. nitida*; and the cheliped is 1.5 times as long as the carapace length in *M. verrilli*, but about the same length in *M. ciliata* and *M. nitida*.

Distribution.—*Munidopsis ciliata* occurs in the eastern part of Cascadia Basin from 2,030 to 2,875 m, off Panama (Faxon 1895) and off the Arrou Islands, Indonesia, (Henderson 1888) in the Pacific Ocean, and the Bay of Bengal, Indian Ocean (Wood-Mason 1891; Alcock 1901). It occurs deeper than *M. verrilli*, which has only been reported off California from San Diego to the Pioneer Seamount at depths of 805-1,618 m (Goodwin 1952). No *M. verrilli* have been found at these depths off Oregon. Goodwin (1952) found *M. verrilli* on rock samples. In one beam trawl (BMT 162) off the Oregon coast, a log was collected at 2,724 m on which there were 33 *M. ciliata*, 67% of the total *M. ciliata* caught.

Munidopsis yaquinensis n. sp. (Figure 5)

Material.—Holotype, USNM 171340, female, 17.4 mm CL, stn CP-3-A, 45°57.1′ N, 127°32.9′ W, BMT 321, 2,763 m; Paratypes: OSUBI 01583, 6 males, 12-13 mm CL, stn CP-1-A, 45°56.5′ N, 125°52.5′ W, BMT 251, 2,377 m.

Diagnosis.—A small species, 12-17 mm CL; large spatulate rostrum with strong carina, small stout eyespines hidden by rostrum; carapace with no spines but covered with small transverse ridges; antennal and anterolateral points of front carapace margin separated by semicircular margin; ambulatory legs with strong anterodorsal carinae.

Description.—Rostrum wide, spatulate, with crenulated edges, base of rostrum with notch around cornea; dorsal surface of rostrum sparsely covered with setae, strong dorsal median carina from anterior part of rostrum to center of gastric area, median carina not extending to tip of rostrum; ventral surface of rostrum covered with small setae and with central ridge; length, 4.9 mm.

Carapace length (17.4 mm) greater than anterior carapace width (8.3 mm), posterior carapace width (11.5 mm), or largest width of carapace (12.2 mm); frontal margin with antennal and anterolateral points separated by semicircular border; lateral margins without spines, forming raised rounded margin; single ridge at posterior border, unarmed; carapace surface covered by small ridges with setae on anterior side, ridges strongly transverse except for those on anterior branchial regions, two larger ridges with crenulated edges on anterior gastric area.

Sternum covered by very small ridges with long setae.

Abdomen unarmed, covered with setae, very slight ridges on somites two and three.

Ocular peduncle movable, with a small, stout, inner eyespine covered by rostrum, eyespine a little longer than length of unpigmented cornea.

Basal segment of antennular peduncle with small anterodorsal spine and anteroventral, jagged, stout tooth.

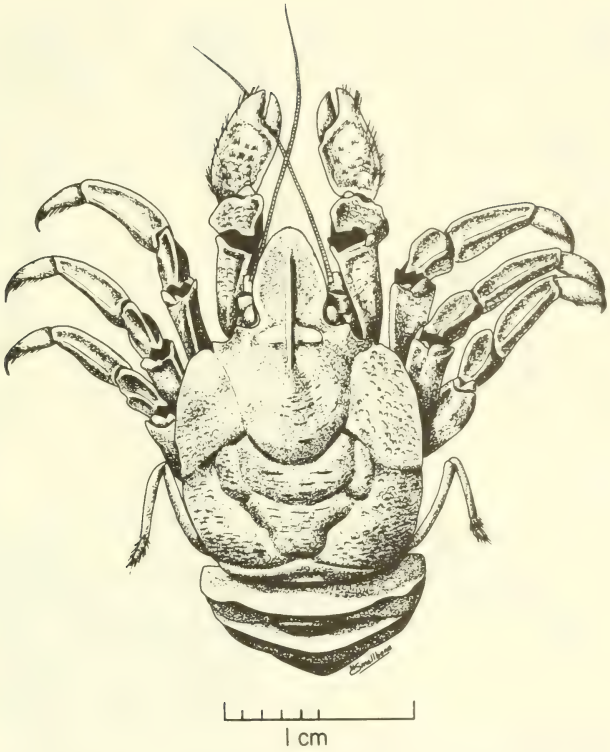


FIGURE 5.—*Munidopsis yaquinensis*, new species, female holotype, dorsal view.

Basal segment of antennal peduncle with two stout teeth; second, third, and fourth segments without teeth or spines; anterior fourth segment with outer rounded extension.

Inner margin of third maxilliped smooth.

Chelipeds with epipodites, chelipeds covered with very small ridges with setae, carpus with strong inner ridge, merus triangular with strong dorsal ridge, right finger length 47% of chela length (6.4 mm), right cheliped length 19.0 mm. Pereiopods without epipodites, covered sparsely with only short setae; propodus, carpus, and merus triangular in cross section, with prominent ridges on anterodorsal side.

Remarks.—The seven Oregon specimens are similar in all important characteristics, with the exception of an OSUBI 01583 specimen, which has an extra long, apparently deformed, rostrum with notched sides.

Munidopsis yaquinensis differs distinctly from all other known species. It most closely resembles *M. platirostris* (Milne-Edwards and Bouvier 1897) and *M. livida* (Pequegnat and Pequegnat 1971).

Etymology.—*Munidopsis yaquinensis* is named for the Oregon State University oceanographic ship RV *Yaquina*.

Distribution.—Occurs at 2,763 and 2,377 m in Cascadia Basin.

Munidopsis cascadia n. sp. (Figure 6)

Material.—Holotype, USNM 171338, female, 54 mm CL, stn CP-1-E, 44°35.5′ N, 125°35.4′ W, OTB 112, 2,810 m; Paratypes: USNM 134658, male, 45 mm CL, stn CP-1-E, 44°46.2′ N, 125°01.8′ W, OTB 49, 2,800 m; USNM 171339, female, 38 mm CL, stn CP-2-A, 45°59.1′ N, 126°40.1′ W, BMT 256, 2,743

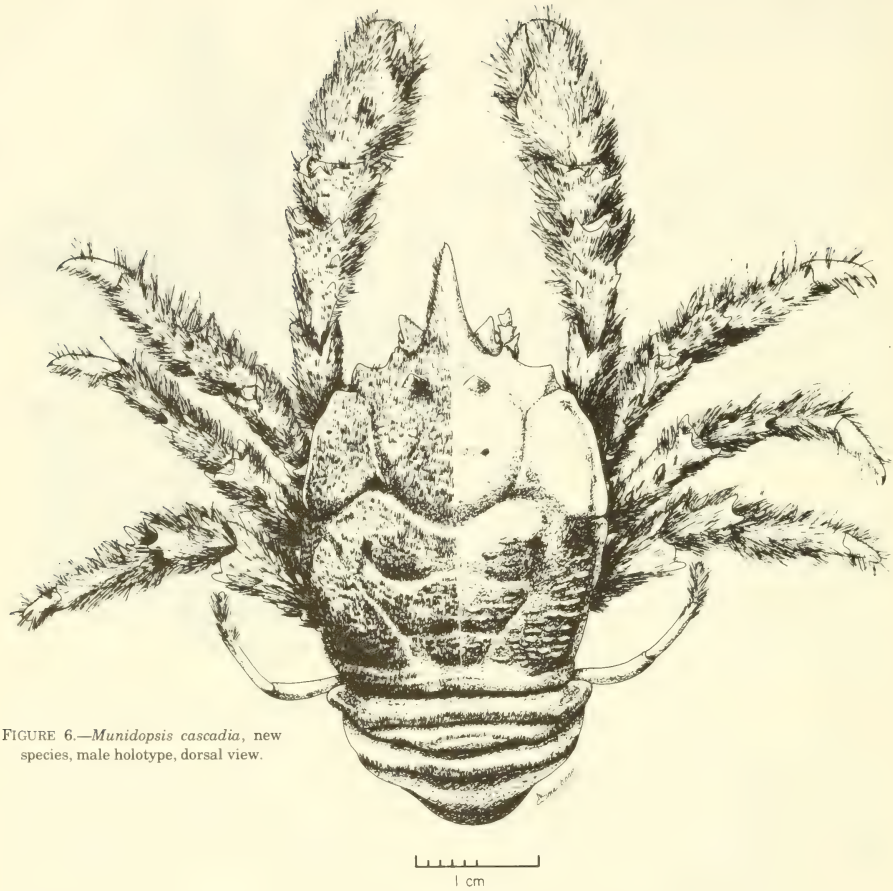


FIGURE 6.—*Munidopsis cascadia*, new species, male holotype, dorsal view.

m; OSUBI 00177, male, 51 mm CL, stn CP-1-E, 44°32.3′ N, 125°41.6′ W, OTB 77, 2,975 m; OSUBI 00178, gravid female, 37 mm CL, stn CP-1-E, 44°48.8′ N, 125°36.4′ W, BMT 287, 2,743 m; OSUBI 00179, male, 27 mm CL, stn CP-2-D, 44°53.7′ N, 126°33.4′ W, BMT 162, 2,884 m; OSUBI 00180, gravid female, 47 mm CL, stn CP-1-D, 44°55.4′ N, 125°40.6′ W, BMT 187, 2,760 m.

Comparative material.—*Munidopsis bermudezi* holotype, MCZ 10231, female, 38 mm CL, stn 2967, 19°43.5′ N, 74°57.5′ W, 2,434-3,020 m.

Diagnosis.—Moderate size (27-54 mm CL); carapace and legs densely covered with setae; stout eyespine on immovable eye stalk; two stout gastric spines; lateral margins of carapace smooth and slightly convex; resembles *Munidopsis bermudezi*.

Description.—Carapace length longer than wide, posterior width slightly greater than anterior width; strong antennal and anterolateral teeth separated by semicircular margin, a blunt tooth distal to anterolateral tooth, another blunt tooth at end of cervical groove; lateral margins raised

and slightly convex; pair of large, blunt, gastric spines, one pit behind each gastric spine, each pit surrounded by a small bare area; dorsal carapace surface densely covered with setae except for bare spots posterior to pits on gastric area, on cervical groove, and on anterior boundary of cardiac region; with setae removed dorsal surface fairly smooth except for rounded tubercles of posterior branchial area; one blunt ridge at unarmed posterior margin.

Rostrum 22% of carapace length, triangular in dorsal view, horizontal in lateral view, covered with setae, bluntly carinate dorsally.

Abdomen densely pubsecent, unarmed; second, third, and fourth somites with two blunt transverse ridges.

Sternum with few setae and small tubercles; with transverse setose ridge opposite legs.

Eyestalks immovable; long, stout, pubescent internal eye spine much longer than diameter of the cornea.

Basal segment of antennular peduncle with one long spine midventrally, one long spine middorsally, and an inner toothed process.

Basal segment of antennal peduncle covered with setae, bearing outer ventral tooth and stout, inner, ventral spine. Second segment with large, outer, ventral spine and small, inner, ventral tooth.

Inner margin or merus of third maxilliped has three main spines, the posterior two have two points.

Cheliped shorter than carapace length; densely pubescent; epipods on chelipeds only; ischium with dorsal and ventral spine at meral articulation and a ventral row of six to seven small spines (including spine at meral articulation); merus with five spines at carpal articulation, dorsal row of six spines (including spine at carpal articulation), and two spines on the inner margin; carpus with four spines at chela articulation and one spine on inner dorsal surface; chela without spines.

Remarks.—Paratypes differ only slightly from holotype (Table 3). The chelipeds of four paratypes (USNM 134658, USNM 171339, OSUBI 00177, and OSUBI 00178) are relatively longer than those of the holotype and two other paratypes (OSUBI 00179 and OSUBI 00180), as shown by the ratio of carapace length to cheliped length in Table 3. In two specimens (OSUBI 00180 and USNM 134658), the lateral carapace margins posterior to the cervical groove have jagged edges instead of being smooth. The number of spines on the inner edge of the merus of the third maxilliped is constant except for one maxilliped of USNM 134658.

The number of spines on the cheliped segments is usually constant. Only the holotype has five spines at the carpal-meral articulation—the paratypes have four. There are four to five spines of the dorsal row on the merus; usually there are four on the paratypes. The number of spines on the ventral row of the ischium is variable, ranging from three to six. The dorsal inner spine on the carpus is always present, but is greatly reduced on paratype OSUBI 00179, and on OSUBI 00177 there are two spines.

A rhizocephalan parasite is present under the abdomen of USNM 171339.

Munidopsis cascadia was compared with the type of *M. bermudezi*. *Munidopsis cascadia* has stouter, blunter gastric spines, no spines on the lateral margin of the carapace, convex rather than a straight lateral margin of the carapace, and more pubescence.

Etymology.—*Munidopsis cascadia* is named from Cascadia Basin since all the specimens were found there.

Distribution.—Only seven specimens of *M. cascadia* are known, all from Cascadia Basin at 2,743-2,926 m. *Munidopsis bermudezi* has only been found in the Atlantic Ocean (Chace 1942;

TABLE 3.—Morphometry of *Munidopsis cascadia*.

Measurement (mm)	USNM [1]171338	USNM 134658	USNM 171339	OSUBI 00177	OSUBI 00178	OSUBI 00179	OSUBI 00180
Carapace length	54	45	38	51	37	27	47
Rostrum length	14	13	10	15	9	8	13
Anterior carapace width	36	21	18	23	17	12	23
Posterior carapace width	38	27	25	32	24	16	36
Cheliped length	43	41	33	49	35	22	37
Chela length	21	19	14	24	12	10	17
Carapace length/cheliped length	1.26	1.10	1.15	1.04	1.06	1.23	1.27

[1]Type-specimen.

Sivertson and Holthuis 1956; Pequegnat and Pequegnat 1970; Laird et al. 1976).

Munidopsis beringana Benedict 1902

Munidopsis beringana Benedict 1902:279 (original description), fig. 23.

Material.—USNM 134659, male 32 mm CL, male, 29 mm CL, female, 29 mm CL, stn Coos Bay #A, 43°17.3′ N, 125°49.3′ W, OTB 76, 3,000 m; OSUBI 00175, female, 31 mm CL, stn CP-2-E, 44°40.8′ N, 126°26.5′ W, OTB 48, 2,800 m; OSUBI 00176, male, 23 mm CL, stn CP-3-D, 44°53.5′ N, 127°27.5′ W, BMT 332, 2,826 m; 20 uncataloged specimens, no ovigerous females.

Remarks.—Three Oregon specimens (USNM 134659) were compared with Benedict's syntypes at the USNM by Henry B. Roberts.[2] He found considerable variation between the Oregon specimens and the syntypes regarding number of spines on the gastric area, length and spacing of the rugae on the carapace, and number of spines on the lateral edges of the carapace and on the meri of the chelipeds. The rugae of the Oregon specimens are, in general, shorter, more prominent, and more widely separated than the rugae of Benedict's specimens from the Bering Sea. The number of spines on the gastric area of the Oregon specimens varied from 4 to 17, on the lateral edge of the carapace from 2 to 4, and on the meri of the chelipeds from 7 to 12.

Distribution.—*Munidopsis beringana* was obtained in the deeper portions of Cascadia Basin from 2,800 to 3,041 m, on Tufts Plain from 3,354 to 3,990 m, and in the Bering Sea at *Albatross* stn 3603, 3,276 m (Benedict 1902).

Munidopsis tuftsi n. sp. (Figure 7)

Material.—Holotype, USNM 171336, male, 70 mm CL, stn TP-3, 44°40.8′ N, 133°26.3′ W, BMT 233, 3,717 m; Paratypes: USNM 171337, male, 36 mm CL, stn TP-4, 44°31.1′ N, 134°43.8′ W, OTB 334, 3,858 m; OSUBI 00181, male, 62 mm CL, stn TP-3, 44°39.8′ N, 133°37.2′ W, BMT 232, 3,724 m; OSUBI 00183, gravid female, 67 mm CL, stn TP-7, 44°58.0′ N, 133°14.5′ W, BMT 302, 3,500 m; OSUBI 01582, male, 15 mm CL, stn TP-6, 44°59.8′ N, 132°12.1′ W, BMT 302, 3,585 m.

Comparative material.—*Munidopsis crassa*: USNM 8563, female 45+ mm CL, *Albatross* stn 2224, 36°16.5′ N, 68°21′ W, 4,710 m; USNM 10803, female, 43 mm CL, *Albatross* stn 2573, 40°34.3′ N, 66°09′ W, 3,188 m; USNM 19289, male 44 mm CL, *Albatross* stn 2566, 37°23′ N, 68°08′ W, 4,795 m. *Munidopsis aculeata*: USNM 21277, male 39 mm CL, *Albatross* stn 3382, 6°21.0′ N, 80°41.0′ W, 3,281 m. *Munidopsis subsquamosa*: See *M. subsquamosa*.

Diagnosis.—Medium-sized species, 36-70 mm CL; triangular rostrum with small lateral spines; long eyespines; carapace wider posteriorly than anteriorly, covered with tubercles, first lateral spine not much larger than anterolateral spine; similar to *Munidopsis crassa*.

Description.—Rostrum triangular, bearing six (two right, four left) small spines laterally on distal half, upturned distally, dorsal median carina; dorsal surface with small tubercles; ventral surface smooth; length 26% of carapace length.

Carapace longer than wide, anterior width and length measured between first lateral spines less than posterior width; frontal margin bearing antennal spines, anterolateral spine on hepatic region with three spinules. First lateral spine on anterior lobe of branchial region with spinules on anterolateral spine. Several (five or six) small spines on lateral edge behind first lateral spine. Gastric area covered by crenulated tubercles bearing setae; six main spines—four at the base of the rostrum, two posterior to these—and numerous slightly smaller spines, smooth spaces between spines and tubercles. Cardiac and posterior branchial areas with crenulated transverse ridges bearing setae, smooth between ridges. Posterior margin unarmed, double ridge of small tubercles.

Sternum smooth, except for scattered setae on bumps and lateral ridges with many setae on top.

Abdomen spineless, covered with tubercles; ridges on somites two to four.

Ocular peduncle slightly moveable, extends beyond unpigmented cornea as stout inner spine, about twice the length of diameter of cornea, spinule on inner side of cornea.

Basal segment of antennular peduncle with one long slender spine midventrally; one long slender

[2]Henry B. Roberts, Senior Museum Specialist, U.S. National Museum, Washington, DC 20560, pers. commun. July 1970.

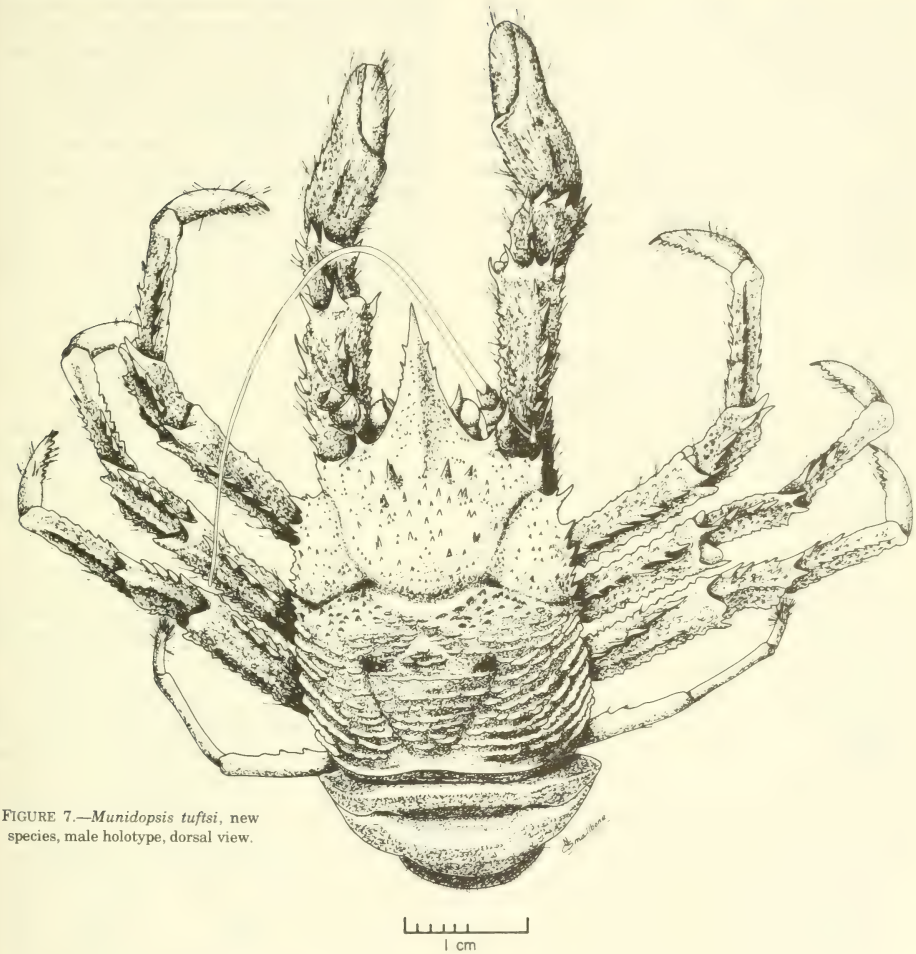


FIGURE 7.—*Munidopsis tuftsi*, new species, male holotype, dorsal view.

spine middorsally; a rounded, toothed process on inner side; and spinule on outer side.

Basal segment of antennal peduncle with two stout ventral spines. Second segment with outer spines and a small dorsal tooth. Third segment with four spines: inner, outer, and smaller dorsal and ventral spines. Fourth segment with two small, blunt, dorsal processes.

Inner margin of merus of third maxilliped with four main spines, plus several spinules.

Chelipeds with epipods. Chelipeds covered with setae and small tubercles, chela bears no major spines; carpus with five small spines at distal edge, and two rows of dorsal spines; merus with three to five small spines at distal edge, row of six to nine spines on dorsal surface, and two inner spines on left merus. Ambulatory legs without epipods, covered with setae and tubercles, and with spines on carina of propodus, carpus, and merus.

Remarks.—The three paratypes vary from the holotype in the number and presence of spinules

and spines. Both the holotype and OSUBI 00181 have spinules on the inner side of the ocular peduncle; OSUBI 00183 has no inner spinule but has an outer spinule; USNM 171337 has no spinules on the ocular peduncle. The number of small spines on the rostrum varies from two to seven with the smallest specimen having only two spines. Paratypes USNM 171337 and OSUBI 00183 have very few spinules on the anterolateral and first lateral spines compared with the other two specimens. The number of spines on the inner margin of the third maxilliped varies from two to four. The specimens are similar in the ornamentation of the carapace and in their proportions (Table 4).

Munidopsis tuftsi belongs to a species complex including *M. crassa*, *M. aculeata*, and *M. subsquamosa*. These species can be separated by observing several characteristics (Table 5). In this complex, *M. tuftsi* most closely resembles *M. crassa*, but differs in having a narrower anterior carapace and narrower width between first lateral spines compared with the posterior carapace width; anterolateral and first lateral spines of the same size; and small spines on the lateral edges of the rostrum. Although *M. tuftsi* has some characteristics in common with *M. aculeata* and *M. subsquamosa*, it has a distinctly more spinous ornamentation on the carapace. A very small specimen of *M. tuftsi*, OSUBI 01582, differs from the larger specimens only in the smoother carapace ornamentation and a larger ratio for anterior carapace width/posterior carapace width (Table 5). The ratio of cornea diameter divided by eyespine length is quite variable for *M. subsquqmosa*, but is usually between 0.46 and 0.55 for *M. crassa* and *M. tuftsi*.

Etymology.—*Munidopsis tuftsi* is named for Tufts Plain where all specimens were collected.

Distribution.—The four specimens of *M. tuftsi* were collected from Tufts Plain at depths of 3,500-3,858 m. *Munidopsis crassa*, the most similar species, has only been found from the Atlantic Ocean (Laird et al. 1976).

TABLE 4.—Morphometry of *Munidopsis tuftsi*.

Measurement (mm)	USNM [1]171336	OSUBI 00181	USNM 171337	OSUBI 00183	OSUBI 01582
Carapace length	70	62	36	[2]67	14.8
Rostrum length	18	17	9	[2]16	4.2
Rostrum length/carapace length	0.26	0.27	0.25	0.24	0.27
Anterior carapace width	30	29	18	32	7.6
Posterior carapace width	41	37	22	42	8.2
Width between first lateral spines	38	36	21	42	8.2
Right cheliped	84	69	43	76	14.1

[1]Holotype.
[2]Rostrum broken at tip.

Munidopsis subsquamosa Henderson 1885

Munidopsis subsquamosa Henderson 1885:414 (original description); Henderson 1888:152 (redescription), pl. 16, fig. 4.
Munidopsis subsquamosa Henderson var. *pallida* Alcock 1894:331 (original description); Alcock 1901:268 (redescription).
Munidopsis geyeri Pequegnat and Pequegnat 1970:149 (original description).

TABLE 5.—Morphometric ratios and spination that distinguishes *Munidopsis tuftsi*, *M. crassa*, *M. aculeata*, and *M. subsquamosa*.

Characteristics	*M. tuftsi*[1]	*M. crassa*[2]	*M. aculeata*[3]	*M. subsquamosa*[4]
1. Chela length/carapace length	0.41-0.44	0.42-0.45	0.65	0.37-0.46
2. Anterior carapace width/posterior carapace width	0.73-0.93	[5]0.90	0.92	0.80-0.98
3. Width between first lateral spines/posterior carapace width	0.93-1.00	1.03-1.13	1.05	1.07-1.25
4. Cornea length/eyespine length	0.48-0.55	0.36-0.49	0.89	0.52-0.82
5. First lateral spine compared with anterolateral spine	Same size	Larger	Same size	Larger
6. Armature on lateral edges of rostrum	Small spines	Minute teeth, none	None	Minute teeth and small spines
7. Rostrum turned up sharply	No	No	Yes	No
8. Number of spines on gastric area	2-6	2-4	6	2-12
9. Ornamentation on gastric area	Tubercles with blunt teeth	Tubercles with blunt teeth	Sparsely covered with small scalelike tubercles	Densely covered with large scalelike tubercles
10. Geographic distribution	Tufts Plain	Off North Carolina, SE of Martha's Vineyard, SE of Georges Bank	Gulf of Panama	Gulf of Panama, Cascadia Basin, Gulf of Mexico, Carribbean

[1]USNM 171336 (holotype), USNM 171337, OSUBI 00181, OSUBI 00183, OSUBI 01582.
[2]USNM 9563 (holotype; measurements from Smith (1885) because holotype is in poor condition), USNM 19289, USNM 10803.
[3]USNM 21277
[4]USNM 21314 (holotype), USNM 171348, OSUBI 00185, OSUBI 00186, OSUBI 00187. *M. geyeri*—USNM 299042, TAMU 2-0574, TAMU 2-0575.
[5]Unknown for holotype.

Material.—*Munidopsis subsquamosa*: Holotype, USNM 21314, female 20 mm CL, *Albatross* stn 3361, 6°10.0′ N, 83°6.0′ W, 2,692 m; USNM 171348, male, 57 mm CL, stn Coos Bay #A, 43°17.3′ N, 125°49.3′ W, OTB 76, 3,000 m; OSUBI 00185, male, 70 mm CL, stn CP-3-C, 45°12.0′ N, 127°32.5′ W, BMT 324, 2,809 m; OSUBI 00186, female with parasite, 41 mm CL, stn NAD 20A, 44°30.1′ N, 125°24.3′ W, OTB 64, 2,772 m; OSUBI 00187, male, 23 mm CL, stn CP-1-E, 44°31.3′ N, 125°35.5′ W, OTB H-1, 2,736 m; OSUBI 00184, male with isopod parasite, stn CP-1-E, 44°40.5′ N, 125°40.0′ W, OTB 18, 2,850 m; 46 uncataloged specimens from off Oregon, smallest ovigerous female 54 mm CL.

Comparative material.—*Munidopsis geyeri*: Holotype, USNM 128812, male, 25 mm CL, *Alaminos* stn 69-A-11-92, 23°30′ N, 95° W, 2,928-3,001 m; TAMU 2-0574, female, 38 mm CL, male, 47 mm CL, *Alaminos* stn 70-A-10-48, 14°29.5′ N, 74°28.8′ W, 4,154 m; TAMU 2-0575, male, 46 mm CL, male, 18 mm CL, *Alaminos* stn 70-A-10-50, 15°50′ N, 77°24.5′ W, 2,654-2,791 m.

Remarks.—*Munidopsis geyeri* found in the Caribbean and Gulf of Mexico is here synonymized with *M. subsquamosa* from the Pacific and with *M. subsquamosa* var. *pallida* from the Indian Ocean. When compared with closely related species (*M. tuftsi, M. aculeata,* and *M. crassa*), *M. geyeri* and *M. subsquamosa* are identical (Table 5). *Munidopsis subsquamosa* and *M. aculeata* have similar carapace ornamentation, but with *M. subsquamosa* the scalelike tubercles are larger and closer together. The two species are also distinguished by characteristics 1, 3, 5, and 7 of Table 5. *Munidopsis crassa* and *M. tuftsi* have smaller, more spiny tubercles on the carapace and usually have longer, stouter eyespines than *M. subsquamosa*.

The distinctions given by Pequegnat and Pequegnat (1970) to distinguish *M. geyeri* from *M. subsquamosa*, and other taxonomic charcteristics were examined on the Oregon specimens of *M. subsquamosa*, the holotype of *M. subsquamosa*, and five specimens of *M. geyeri*, including the holotype. The range of variations of these characteristics for the Oregon specimens included those found for *M. geyeri*, except for the number of teeth on the lateral edges of the rostrum (Table 6). With the addition of the Oregon specimens, the maximum size and range of variation of *M. subsquamosa* is extended. Mayo (1974), who collected three specimens of *M. geyeri*, proposed that *M. geyeri* might become a synonym of *M. subsquamosa* when more material was available.

Alcock (1894, 1901) stated that *M. subsquamosa* var. *pallida* differs from *M. subsquamosa* by the former having only two spines on the gastric area of the carapace. Henderson (1885) did not state how many gastric spines the holotype has; I found only two.

Five of the Oregon female specimens have rhizocephalan parasites on the ventral side of the abdomen. Two other specimens had isopod parasites under the carapace on the posterior branchial area.

Distribution.—*Munidopsis subsquamosa* occurs mainly in the eastern part of Cascadia Basin from 1,829 to 3,000 m. This species is cosmopolitan, since it has also been collected at 3,431 m off Yokohama, Japan (Henderson 1888), 1,471 and 1,672 m off Panama (Faxon 1895), 3,299 m in the Bay of Bengal (Alcock 1894, 1901), 2,938-3,001 m in the southwest Gulf of Mexico (Pequegnat and Pequegnat 1970), 4,154 m in the Colombian Basin (Pequegnat and Pequegnat 1971), 2,790-2,650 m south of Jamaica (Pequegnat and Pequegnat 1971), and 3,111-3,496 m off Haiti (Mayo 1974).

Munidopsis verrucosus Khodkina 1973

Munidopsis verrucosus Khodkina 1973:1156-1159 (original description), fig. 1, 2.

Material.—*Munidopsis verrucosus*, USNM

TABLE 6.—Selected spine counts for *Munidopsis geyeri* and *M. subsquamosa*.

Characteristic	*M. geyeri*		*M. subsquamosa*		
	Type USNM 289042 (n = 1)	TAMU 2-0574 TAMU 2-0575 (n = 4)	Type USNM 21314 (n = 1)	Oregon specimens (n = 20) Mean	Range
Number of spines on 3d maxilliped (total, right + left)	9	8-10	6	7.8	6-11
Total number of teeth on lateral edges of rostrum	18	7-19	6	3.1	0-6
Number of spines on gastric area of carapace	2	[1]2	2	4.8	2-12
Number of spines behind anterolateral spine of carapace (total, right + left)	4	4-8	2	9.2	4-12

[1] Gastric area of carapace cracked on one specimen.

171347, gravid female, 25 mm CL, Gorda Ridge, 40°13.4′ N, 126°30.0′ W, OTB 104, 4,260 m; OSUBI 00172, female, 26 mm CL, stn TP-9, 45°01.1′ N, 135°12.6′ W, BMT 308, 3,932 m.

Remarks.—The Oregon specimens are indistinguishable from those described by Khodkina (1973). *Munidopsis verrucosus* is very similar to *M. granosa*, but differs in having an epipodite on the cheliped, setae on the tubercles of the carapace, plumose setae on portions of the chelipeds and pereiopods, no small antennal tooth, and no dorsal carina on the rostrum.

Distribution.—Khodkina (1973) collected three male specimens of *M. verrucosus* (33.8 mm, 34.8 mm, and 40.6 mm CL) from the Atakamsky Trench off Antofagasta, Chile, at two stations (lat. 23°47.1′ S, long. 71°03.2′ W, 4,300 m, and lat. 23°15.1′ S, long. 71°39.1′ W, 4,880 m). The two Oregon specimens were also found at great depths—3,932 m on Tufts Plain and 4,194 m on Gorda Ridge off northern California. Alcock (1901) collected one male specimen of *Munidopsis granosa* from 2,812 m in the Bay of Bengal.

Munidopsis latirostris (Henderson) Faxon 1895

Elasmonotus latifrons. Henderson 1885:416 (original description); Henderson 1888:160 (redescription), pl. 19, fig. 1.

Orophorhynchus latifrons. Milne-Edwards and Bouvier 1894:287 (in key to *Orophorhynchus*).

Munidopsis latirostris. Faxon 1895:81-82, 99 (changed name because genus synonomy caused prior usage of *M. latifrons*).

Material.—USNM 21285, female, 15 mm CL, *Albatross* stn 3381, 4°56.0′ N, 80°52.5′ W, 3,243 m; MCZ 4563, female, 16 mm CL, *Albatross* stn 3391, 7°15.0′ N, 79°36.0′ W, 280 m; USNM 171341, 14 specimens, stn CP-1-E, 44°28.2′ N, 125°32.3′ W, OTB 50, 2,800 m; OSUBI 00190, 28 specimens, stn CP-1-E, 44°35.7′ N, 125°34.3′ W, OTB 155, 2,830 m; OSUBI 00191, gravid female, 23 mm CL, male, 22 mm CL, male, 20 mm CL, stn C-P-3E Channel, 44°41.2′ N, 127°21.2′ W, BMT 407, 3,041 m; 541 uncataloged specimens from off Oregon, smallest ovigerous female 18 mm CL.

Remarks.—The characteristics of the Oregon specimens agree with those of the USNM and the MCZ specimens, but differ slightly from the type description (Henderson 1888). The "two slightly rounded elevations" at the base of the rostrum on the gastric area are blunt spines in the observed specimens. The "faint median carina" on the rostrum is a definite rounded ridge extending from the end of the rostrum to the blunt gastric spines (Figure 8).

The following observations are added to Henderson's description of *M. latirostris*. The basal segment of the antennular peduncle is swollen with two outer spines. The basal segment of the antennal peduncle has an outer tooth and an inner spine; the second segment has an outer stout tooth. The meri of the ambulatory legs have dorsal ridges with setae on the anterior side. Epipods are present on the chelipeds only.

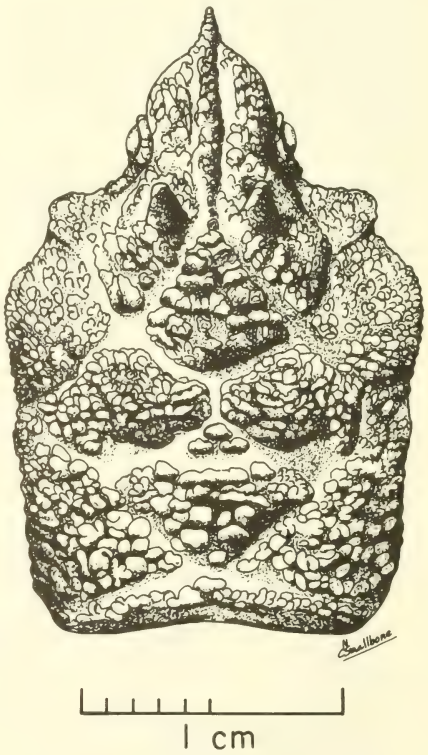


FIGURE 8.—*Munidopsis latirostris*, dorsal view of carapace.

In all specimens examined, the ocular peduncle extends beyond the eye as a blunt spine, although Benedict (1902) does not consider it an eyespine in his key. On the carina of the second, third, and fourth abdominal somites, there are slight median projections. Benedict (1902) considers these projections "armature on the abdomen confined to the median line."

The main variation of the Oregon and *Albatross* specimens is in the shape of the apex of the rostrum. Henderson (1888, plate XIX, figure 1) describes the rostrum as ending in an "acute apex," which is true for USNM 21285 and some of the Oregon specimens. In most of the Oregon specimens and MCZ 4563, the rostrum ends as a spine (Figure 9).

Rhizocephalan parasites occurred under the abdomen in 40 of 444 Oregon specimens; 23 hosts were females and 17 were males.

Distribution.—*Munidopsis latirostris* is the most abundant *Munidopsis* species found in Cascadia Basin, with a wide depth range, 1,900-3,021 m. This species has also been found in the tropical Pacific Ocean at 280 and 3,243 m off Panama (Faxon 1895) and at 1,958 m between Papua and Admiralty Islands (Henderson 1888).

VERTICAL AND GEOGRAPHIC DISTRIBUTION OF THE SPECIES

Twelve species of *Munidopsis* were captured in 51% or 146 of the total number of tows. Collections from both otter and beam trawls are included in the distributional analysis for more complete coverage. Although samples from otter trawls have been considered quantitative (number per hour trawled, Haedrich et al. 1975), beam trawls were designed to be more quantitative, giving number per square meter (Carey and Heyamoto 1972). Carney (1976) questioned the reliability of beam trawl data for area covered and expressed abundance as number per trawl for samples with similar wheel readings. In this paper, abundances are expressed as average number per trawl (number of specimens/number of trawls towed) because beam and otter trawls were towed for approximately the same time. Some specimens which can escape through 1.3 cm mesh liners are not sampled adequately. Adult densities of small species such as *M. ciliata, M. quadrata,* and *M. yaquinensis*, and immature individuals of the other species are probably underestimated. Immature specimens included *M. subsquamosa, M. latirostris, M. bairdii, M. tuftsi*, and *M. beringana*.

FIGURE 9.—*Munidopsis latirostris*, variation in rostrum, left rostrum ends as spine, right rostrum ends as acute apex.

Cascadia Basin off Oregon was probably the only area trawled adequately enough to sample all the species, since most species were collected at least several times there. The most abundant species, *M. latirostris*, contributed 73.0% of the total number of specimens. Three species together contributed 20.2% of the total: *M. bairdii* (7.5%), *M. ciliata* (6.2%), and *M. subsquamosa* (6.5%). These four species together represented 93.2% of all specimens, and were only found in Cascadia Basin. At the deepwater dumpsite stations in northern Cascadia Basin, all of the above except *M. ciliata* were collected. Five additional species (32 specimens) were also found on Cascadia Basin. Although 106 tows were taken on the continental slope off Oregon, only 5 tows yielded a total of three species (six specimens). Three species (17 specimens) were found on Tufts Plain (Table 7).

Abundances (number per trawl) for all *Munidopsis* species were about the same for the base of the continental slope (CP-1 line) and the CP-2 line (Table 7). However, the relative abundance of species changed from east to west. *Munidopsis latirostris* was the most abundant on both the CP-1 and CP-2 lines. On the CP-1 line, *M. subsquamosa* was second in rank, but on the CP-2 line, *M. subsquamosa* was fourth, *M. ciliata* was second, and *M. bairdii* was third (Table 7).

Eight of the 12 *Munidopsis* species were collected in Cascadia Basin, especially below 2,250 m (Figure 10). The single sample from Gorda Ridge, south of Cascadia Basin, contained one specimen of the rare, deepwater form, *M. verrucosus*. *Munidopsis quadrata* was the only species occurring over a wide depth range on the continental slope. A single tow on the lower part of the continental slope contained *Munidopsis* sp. and *M. subsquamosa*.

TABLE 7.—Occurrence of *Munidopsis* species on the continental slope, Cascadia Basin, and Tufts Plain (Figure 1).

Species	Total	Continental slope	Base of continental slope (CP-1, CP-x)	Cascadia Basin (CP-2)	Cascadia Basin (CP-3, CP-4)	Northern Cascadia (DWD)	Tufts Plain (TP-A, TP-B, TP-C)	Gorda Ridge
	number of specimens collected							
M. latirostris	586	0	362	132	77	15	0	0
M. bairdii	60	0	8	45	4	3	0	0
M. ciliata	50	0	2	48	0	0	0	0
M. subsquamosa	52	1	24	15	1	11	0	0
M. beringana	25	0	7	2	5	0	11	0
M. cascadia	7	0	4	3	0	0	0	0
M. yaquinensis	7	0	6	0	1	0	0	0
M. quadrata	6	4	0	0	0	2	0	0
M. tuftsi	5	0	0	0	0	0	5	0
M. aries	2	0	0	1	1	0	0	0
M. verrucosus	2	0	0	0	0	0	1	1
Munidopsis sp.	1	1	0	0	0	0	0	0
Total no. of *Munidopsis* spp	803	6	413	246	89	31	17	1
Mean no./trawl	2.8	0.1	5.1	6.5	2.3	3.1	0.9	1.0
Total no. of trawls	289	106	81	38	38	10	18	1
Percent trawls with *Munidopsis* spp.	51	5	70	87	79	60	78	trace

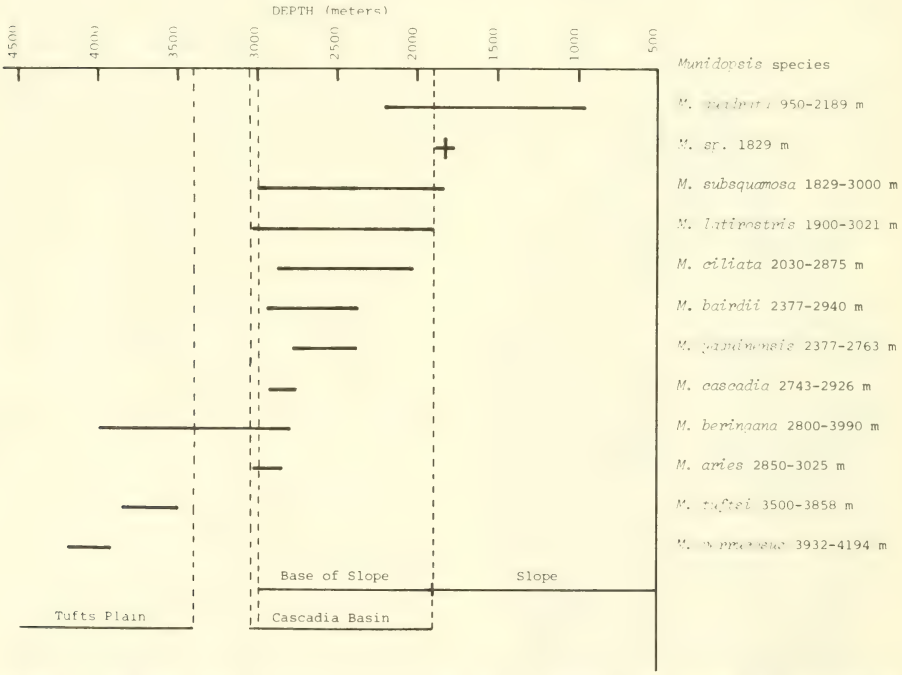


FIGURE 10.—Bathymetry of *Munidopsis* species from the continental slope, Cascadia Basin, and Tufts Plain off Oregon and Washington.

Four types of species distribution patterns emerge when all the stations on Cascadia Basin and Tufts Plain are considered (Figure 11). Two species, *M. latirostris* and *M. bairdii*, were found at most stations sampled in Cascadia Basin. The most abundant species, *M. latirostris*, was also the most widespread since it occurred at all but two of the Cascadia Basin stations. It occurred at

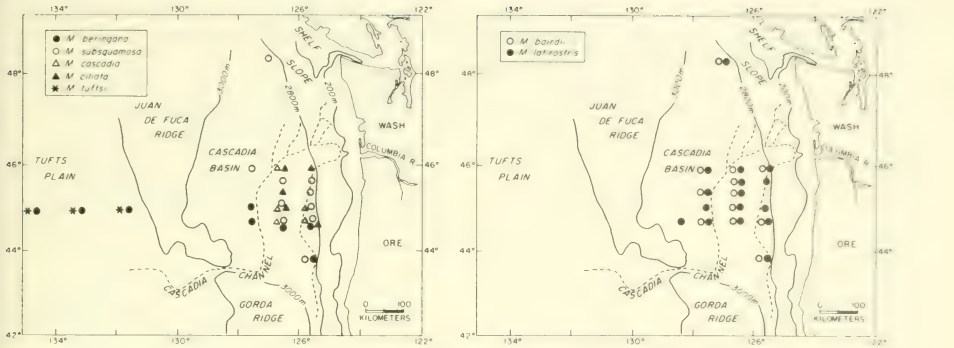


FIGURE 11.—Distribution of *Munidopsis* species off Oregon and Washington; upper—*M. cascadia*, *M. ciliata*, *M. tuftsi*, *M. subsquamosa*, and *M. beringana;* lower—*M. bairdii* and *M. latirostris*.

CP-4-E, the deepest and most western station on Cascadia Basin. Three species—*M. subsquamosa, M. cascadia*, and *M. ciliata*—occurred predominantly on the eastern side of Cascadia Basin. Only *M. beringana* was taken on both abyssal plains, notably occurring in Cascadia Basin only at the deeper, southern stations. Two species occurred only on Tufts Plain—*M. verrucosus* and *M. tuftsi*.

Carney (1976) found greater overlap in species distributions between Cascadia Basin and Tufts Plain for holothurians than for *Munidopsis* species. He described three basic distribution patterns: 1) present on Cascadia Basin but generally absent from the base of the continental slope, 2) present over all of Cascadia Basin extending to the eastern edge of Tufts Plain, and 3) present in the deepest and farthest offshore stations of Cascadia Basin and on Tufts Plain.

Two distributional studies of infauna on Cascadia Basin have shown great variation in species composition between different stations: Hancock's (1969) polychaete study along the CP-E line (Newport hydrographic line) and the gammarid amphipod study at stations CP-1-E and CP-3-E by Dickinson and Carey (1978). Carney (1976) showed that the species composition of polychaetes had greater variability between stations than that of the holothurians. Of the 20 most abundant gammarid amphipod species at the two Cascadia Basin stations, only 6 had similar abundances at both stations, and 10 species only occurred at one station (Dickinson and Carey 1978). Of the eight *Munidopsis* species I found on Cascadia Basin, only three occurred at both CP-1-E and CP-3-E. In all three groups (polychaetes, amphipods, galatheid crabs), there are differences in species composition between stations on either side of Cascadia Basin, which Dickinson and Carey (1978) suggested may be caused by decreasing sedimentation rates with increasing distance offshore, since other environmental conditions are constant across Cascadia Basin.

Of 65 known abyssal species of *Munidopsis*, Doflein and Balss (1913) found that a high percentage (71%) are endemic to specific oceanic regions. Since many abyssal species have been described from single or few specimens, the percentage of endemism declines with further collecting. My collections off Oregon extended the geographic range of seven species, three of which were previously known from only one location: *M. beringana* from the Bering Sea, *M. aries* from the Caribbean, and *M. verrucosus* from off Chile.

The number of cosmopolitan *Munidopsis* species, those found in all three major oceans, is small (Doflein and Balss 1913). Only one of the Oregon species, *M. subsquamosa*, can be considered cosmopolitan. Seven of the Oregon species are found only in the Pacific Ocean; one is also found in the Indian Ocean (Table 8). However, four of the Pacific and Indian-Pacific species have sibling species in the Atlantic Ocean, evidence that at one time the progenitors had broader distributions.

The four most abundant species from Cascadia Basin have tropical Pacific affinities (Table 8). Only one species, *M. beringana*, has arctic affinities and is found in the deepest parts of Cas-

TABLE 8.—Geographic occurrences of *Munidopsis* species from Cascadia Basin and Tufts Plain (Milne-Edwards 1880; Smith 1884, 1886; Henderson 1888; Faxon 1895; Alcock 1901; Benedict 1902; Rathbun 1904; Kensley 1968; Pequegnat and Pequegnat 1970, 1971; Khodkina 1973; Mayo 1974; Laird et al. 1976).

	Eastern Pacific Ocean					World ocean			Sibling species[1]	
Species	Endemic	North America	Arctic	Tropical	Bipolar	Pacific	Indian and Pacific	Atlantic	Species	Ocean
M. aries								+	—	—
M. bairdii				-				+	—	—
M. beringana			+			+			—	—
M. cascadia	+					+			*M. bermudezi*	Atlantic (Laird et al. 1976)
M. ciliata				+			-		*M. nitida*	Atlantic (Pequegnat and Pequegnat 1970)
M. latirostris				+		+			—	—
M. quadrata		+				+			—	—
M. subsquamosa				+			+	+	—	—
M. tuftsi	+					+			*M. crassa*	Atlantic (Laird et al. 1976)
M. verrucosus					-	+			*M. granosa*	Indian (Alcock 1901)
M. yaquinensis	+					+			—	—

[1]Most similar species, as described in this paper.

cadia Basin and on Tufts Plain. *Munidopsis verrucosus*, another deepwater species, may have a bipolar distribution since its only other known occurrence is in the Peru-Chile trench. The three new species may be endemic, but two of them have sibling species in the Atlantic Ocean. *Munidopsis quadrata* is only found off the west coast of North America from Washington to Mexico. Of the five species occurring off California and Mexico (Schmitt 1921; Haig 1956), *M. quadrata* is the only one whose range extends north to Oregon and Washington.

ACKNOWLEDGMENTS

I am grateful to James E. McCauley and David L. Stein for their taxonomic advice and critical review of the paper, and to Andrew G. Carey for providing the galatheid crabs for this study. For loans of specimens, I thank Raymond B. Manning of the U.S. National Museum, Herbert W. Levi of the Museum of Comparative Zoology at Harvard University, and Linda and Willis Pequegnat of Texas A&M University. I appreciate Linda H. Pequegnat's review of the manuscript. Ken Johnson translated a French article, Gary A. Halvorson translated a Russian article, and Kathy Jefferts latinized names of the new species. My special thanks go to Norma C. Smallbone for the excellent drawings.

I thank the following people with pleasure for their work at sea and in the laboratory over the years: Mimi Alspaach Alton, Frances Bruce Pope, Nikki Cummins, Carolyn Kuelthau Evans, Mike Kyte, Roger Paul, Gene Ruff, and the officers and crews of the RV *Yaquina* and RV *Cayuse*.

This research was supported by: the Oceanography Section, National Science Foundation, NSF grant GB-4629; the Atomic Energy Commission, Contracts AT (45-1)1750 and AT (45-1)2227, Task Agreement 12; and the Office of Naval Research, through contract N000 14-67-A-0369-0007 under project NR083-102. Ship support was partially supplied by the National Science Foundation Grant OCE 76-00061. The ERDA publication number is RLO-2227-T12-77.

LITERATURE CITED

ALCOCK, A.
1894. Natural history notes from H. M. Indian Marine Survey Steamer *"Investigator,"* Commander R. F. Hoskyn, R. N., late commanding. Series II, No. 1. On the results of the deep-sea dredging during the season 1890-91 (continued). Ann. Mag. Nat. Hist., Ser. 6, 13:321-334.
1901. A descriptive catalogue of the Indian deep-sea crustacea decapoda and anomala in the Indian Museum. Indian Med. Serv., Calcutta, p. 1-286.

BAHAMONDE, N.
1964. Dos nuevos *Munidopsis* en aguas chileans (Crustacea Decapoda, Anomura). Bol. Mus. Nac. Chile 28(4):157-170.

BENEDICT, J. E.
1902. Descriptions of a new genus and forty-six new species of crustaceans of the family Galatheidae, with a list of the known marine species. Proc. U.S. Natl. Mus. 26:243-344.

CAREY, A. G., JR., AND H. HEYAMOTO.
1972. Techniques and equipment for sampling benthic organisms. *In* A. T. Pruter and D. L. Alverson (editors), The Columbia River estuary and adjacent ocean waters, bioenvironmental studies, p. 378-408. Univ. Wash. Press, Seattle.

CAREY, A. G., JR., J. B. RUCKER, AND R. C. TIPPER.
1973. Benthic ecological studies at deepwater dumpsite G in the Northeast Pacific Ocean off the coast of Washington. *In* G. A. Young (compiler), Proceedings of

the first conference on the environmental effects of explosives and explosions (May 30-31, 1973), p. 120-137. NOL Tech. Rep.

CARNEY, R. S.
1976. The patterns of abundance and relative abundance of benthic holothurians (Echinodermata: Holothuroidea) on Cascadia Basin and Tuft's Plain in the northeast Pacific. Ph.D. Thesis, Oregon State Univ., Corvallis, 185 p.

CHACE, F. A., JR.
1942. Reports on the scientific results of the Atlantic expeditions to the West Indies, under the joint auspices of the University of Havana and Harvard University. The Anomuran Crustacea. I. Galatheidea. Torreia 11, 106 p.

CORLISS, J. B., AND R. D. BALLARD.
1977. Oases of life in the cold abyss. Natl. Geogr. Mag. 152:441-451.

DICKINSON, J. J., AND A. G. CAREY, JR.
1978. Distribution of gammarid Amphipoda (Crustacea) on Cascadia Abyssal Plain (Oregon). Deep-Sea Res. 25:97-106.

DINKINS, S.
1969. Lanzarote the strangest Canary. Natl. Geogr. Mag. 135:116-139.

DOFLEIN, F., AND H. BALSS.
1913. Die Galatheiden der Deutschen tiefsee-expedition. Wiss. Ergeb. dt. Tiefsee-Exped. "Valdivia" 20:130-184.

FAXON, W.
1893. Reports on the dredging operations off the west coast of Central America to the Galapagos, to the west coast of Mexico, and in the Gulf of California, in charge of Alexander Agassiz, carried on by the U.S. Fish Commission Steamer "*Albatross*," during 1891 Lieut.-Commander Z. L. Tanner, U.S.N., Commanding. VI. Preliminary descriptions of new species of Crustacea. Bull. Mus. Comp. Zool. 24:149-220.
1895. Reports on an exploration off the west coasts of Mexico, Central and South America, and off the Galapagos Islands, in charge of Alexander Agassiz, by the U.S. Fish Commission Steamer "*Albatross*," during 1891, Lieut.-Commander Z. L. Tanner, U.S.N., commanding. XV. The stalk-eyed crustacea. Mem. Mus. Comp. Zool. Harv. 18:1-292.

GOODWIN, D. G.
1952. Some decapod Crustacea dredged off the coast of central California. Proc. Calif. Acad. Sci. 27:393-397.

HAEDRICH, R. L., G. T. ROWE, AND P. T. POLLONI.
1975. Zonation and faunal composition of epibenthic populations on the continental slope south of New England. J. Mar. Res. 33:191-212.

HAIG, J.
1956. Notes on two anomuran crustaceans new to California waters. Bull. South. Calif. Acad. Sci. 55(2):79-82.

HANCOCK, D. R.
1969. Bathyal and abyssal polychaetes (Annelids) from the central coast of Oregon. M.S. Thesis, Oregon State Univ., Corvallis, 121 p.

HENDERSON, J. R.
1885. Diagnoses of the new species of Galatheida collected during the "*Challenger*" expedition. Ann. Mag. Nat. Hist., Ser. 5, 16:407-421.
1888. Report on the anomura collected by H.M.S. Challenger during the years 1873-76. Rep. Sci. Res. H.M.S. Challenger, Zoology 27 (part 69):1-221.

KENSLEY, B. F.
1968. Deep sea decapod crustacea from west of Cape Point, South Africa. Ann. S. Afr. Mus. 50:283-323.

KHODKINA, I. V.
1973. New species of the genus *Munidopsis* (Decapoda, Anomura) from the east Pacific. Zool. Zh. 52:1156-1167.

LAIRD, C. E., E. G. LEWIS, AND P. A. HAEFNER, JR.
1976. Occurrence of two galatheid crustaceans, *Munida forceps* and *Munidopsis bermudezi*, in the Chesapeake Bight of the western North Atlantic Ocean. Fish. Bull., U.S. 74:462-463.

MAYO, B. S.
1974. The systematics and distribution of the deep-sea genus *Munidopsis* (Crustacea, Galatheidae) in the western Atlantic Ocean. Ph.D. Thesis, Univ. Miami, Coral Gables, 432 p.

MILNE-EDWARDS, A.
1880. Reports on the results of dredging under the supervision of *Alexander Agassiz*, in the Gulf of Mexico, and in the Caribbean Sea 1877, '78, '79, by the U.S. Coast Survey Steamer "*Blake*," Lieut.-Commander C. D. Sigsbee, U.S.N., and Commander J. R. Bartlett, U.S.N., commanding. VIII. Études préliminaires sur les Crustacés. Bull. Mus. Comp. Zool. Harv. 8:1-68.

MILNE-EDWARDS, A., AND E.-L. BOUVIER.
1894. Considérations générales sur la Famille des Galathéidés. Ann. Sci. Nat., Zool., Ser. 7, 16:191-327.
1897. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877-78), in the Caribbean Sea (1878-79), and along the Atlantic coast of the United States (1880), by the U.S. Coast Survey Steamer "*Blake*," Lieut.-Commander C. D. Sigsbee, U.S.N., and Commander J. R. Bartlett, U.S.N., commanding. XXXV. Description des Crustacés de la famille des Galathéidés recueillis pendant l'expédition. Mem. Mus. Comp. Zool. Harv. 19:1-141.

PEQUEGNAT, L. H., AND W. E. PEQUEGNAT.
1970. Deep-sea anomurans of superfamily Galatheoidea with descriptions of three new species. *In* W. E. Pequegnat and F. A. Chase, Jr. (editors), Contributions on the biology of the Gulf of Mexico, p. 125-170. Gulf Publ. Co., Houston, Tex.

PEQUEGNAT, W. E., AND L. H. PEQUEGNAT.
1971. Contributions on the biology of the Gulf of Mexico. Texas A&M Univ. Oceanogr. Stud. 1 (suppl.), 24 p.
1973. *Munidopsis albatrossae*, a new species of deep-sea Galatheidae (Decapoda, Anomura) from the eastern Pacific Ocean. Crustaceana 24:163-168.

RATHBUN, M. J.
1904. Decapod crustaceans of the northwest coast of North America. Harriman Alaska Exped. 10:1-210.

SCHMITT, W. L.
1921. The marine decapod crustacea of California with special reference to the decapod crustacea collected by the United States Bureau of Fisheries Steamer "Albatross" in connection with the biological survey of San Francisco Bay during the years 1912-1913. Univ. Calif. Publ. Zool., 23, 470 p.

SIVERTSEN, E., AND L. B. HOLTHUIS.
1956. Crustacea Decapoda (the Penaeidea and Stenopodidea excepted). Rep. Sci. Res. "Michael Sars" N. Atl. Deep-Sea Exped. 5(12):1-54.

SMITH, S. I.
1883. Preliminary report on the Brachyura and Anomura dredged in deep water off the south coast of New England by the United States Fish Commission in 1880, 1881, and 1882. Proc. U.S. Natl. Mus. 6:1-57.

1884. Report on the decapod crustacea of the Albatross dredgings off the east coast of the United States in 1883. U.S. Comm. Fish Fish., Rep. Comm. 10:345-426.

1885. On some new or little known decapod crustacea from recent Fish Commission dredging off the east coast of the United States. Proc. U.S. Natl. Mus. 7:493-511.

1887. Report on the decapod crustacea of the Albatross dredgings off the east coast of the United States during the summer and autumn of 1884. U.S. Comm. Fish Fish., Rep. Comm. 13:605-705.

TIRMIZI, N. M.
1966. Crustacea: Galatheidae. Br. Mus. (Nat. Hist.) John Murray Exped. 1933-34, Sci. Rep. 11:169-234.

WHITEAVES, J. F.
1874. On recent deep-sea dredging operations in the Gulf of St. Lawrence. Am. J. Sci., Ser. 3, 7:210-219.

WOOD-MASON, J.
1891. Natural history notes from H. M. Indian Marine Survey Steamer "*Investigator*," Commander R. F. Hoskyn, R.N., commanding.—No. 21. Note on the results of the last season's deep-sea dredging. Ann. Mag. Nat. Hist., Ser. 6, 7:186-202.

USING MARKOV DECISION MODELS AND RELATED TECHNIQUES FOR PURPOSES OTHER THAN SIMPLE OPTIMIZATION: ANALYZING THE CONSEQUENCES OF POLICY ALTERNATIVES ON THE MANAGEMENT OF SALMON RUNS

ROY MENDELSSOHN[1]

ABSTRACT

The mathematics of Markov decision processes and related techniques are used to analyze a model relevant to salmon management. It is shown that the choice of grid can have a significant effect on the results obtained. Optimal policies that maximize total expected discounted return may be too variable. Smoothing costs are included to trade off long-run total return against the smoothness of the year-to-year fluctuations in the allowed harvest. Simpler, approximate policies that have a smoothing effect are also found. Preliminary analysis suggests the results are robust against misspecification of the parameters of the model. Concepts such as maximum sustainable yield would seem to impute a very high smoothing cost and are probably not practical for fish populations with a significant degree of randomness.

The history of most managed natural populations is one of sizable, nondeterministic variations in the dynamics of the population. This observed variation tends to have two sources: The first source is actual randomness in the system, such as that due to environmental variability, which will exist no matter how accurate our models become; and the second source is the inaccurate or incomplete specification of the transition probabilities themselves. Standard production models (Schaefer 1954; Pella and Tomlinson 1969; Fox 1970, 1971, 1975) assume deterministic dynamics, as do most recent bioeconomic analyses, as in Clark (1976) or Anderson (1977). For randomly varying populations, at best only extremely low harvests may be sustainable year to year, and it is not difficult to develop realistic scenarios where policies that are sustainable in a deterministic model would cause possible depletion in a stochastic model.

In this paper, the latest tools from stochastic optimization, particularly in the area of Markov decision problems (MDP's) are used to analyze a model relevant to salmon management. The viewpoint taken is that of the analyst, who must analyze trade offs and provide a decision maker with as few policies as possible that contain the maximum amount of information, rather than that of the decision maker, who ultimately decides if a particular concern or trade off is worthwhile. The salmon model is used as an example—the goal is to gain insight into managing randomly varying populations.

Ricker (1958) appears to be the first to examine the effects of variability on management. He used intuition and simulation to arrive at policies that are of the same general form as many of the policies to be discussed in this paper. However, Ricker presented no systematic way of developing optimal policies and made the incorrect assumption that the long-run stochastic behavior will have a mean equal to the deterministic equilibrium yield, with noise around this mean.

Reed (1974) derived qualitative properties of optimal policies if the random variable has a mean of 1, if it affects the population dynamics in a multiplicative manner, and if it has costs when the system is shut down (no harvesting) and then started up again (resumption of harvesting). Reed's results are not relevant to the model discussed in this paper, since he assumed the deterministic population model is concave, while the models examined in what follows are pseudoconcave. A more complete treatment of one dimensional stochastic growth models can be found in Mendelssohn and Sobel (in press).

Walters (1975) and Walters and Hilborn (1976, 1978) discussed a variety of topics as the concerns

[1]Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96812.

Manuscript accepted September 1979.
FISHERY BULLETIN: VOL. 78, NO. 1, 1980.

of this paper. Some of the techniques they discussed, particularly the filtering techniques (Walters and Hilborn 1978), are only appropriate if the model has an additive error term. While a Ricker spawner-recruit curve can be transformed to an additive model, many models do not have this feature.

I am presenting what I feel is an improved way to smooth out the fluctuations in the year-to-year harvests as compared with the method suggested in Walters (1975) and show that the Bayesian (adaptive) model discussed in Walters and Hilborn (1976) has an optimal policy with a very simple form that can be readily calculated.

Moreover, a rigorous approach is taken to define the model on a grid and the effects of the grid choice. None of the papers cited deal with this important question; new results are presented which show that the most serious effect of the grid is on the estimates of the long-run (ergodic) probabilities of the population dynamics when following a given policy. Particularly the tail properties of the ergodic distribution, i.e., the long-run probability of low harvest or low population sizes, are misestimated. This is a new finding even in the MDP literature, and has numerical implications, particularly when calculating the trade off between the mean harvest of a given policy and the long-run probability of undesirable events when following that policy.

THE MODEL

The models to be analyzed were developed by Mathews (1967) to describe the spawner-recruit relationships of sockeye salmon, *Oncorhynchus nerka*, populations in two rivers that run into Bristol Bay, Alaska. Oceanographic and other factors affect the number of recruits to a degree where the relationships can be modeled by the random equations:

Wood River:

$$x_{t+1} = \exp(d)\,(4.077 y_t)\exp(-0.800 y_t)$$
$$d \approx N(0, 0.2098) \qquad (1.1a)$$

Branch River:

$$x_{t+1} = \exp(d)\,(4.554 y_t)\exp(-1.845 y_t)$$
$$d \approx N(0, 0.3352) \qquad (1.1b)$$

where y_t is the number of spawners in period t, x_{t+1} is the (random) number of recruits in period $t+1$, and $d \approx N(a, b)$ denotes that d is a normally distributed random variable, with mean a and variance b.

For deterministic versions of Equation (1.1), the primary objective of management is MSY (maximum sustainable yield), which is equivalent to the largest per period growth of the deterministic model. The stochastic equivalent of this criterion is to maximize the average per period harvest, or gain optimality. Mathematically, letting E be the expectation operator, this is

$$\max \lim_{T\to\infty} \left[\frac{1}{T} E \sum_{t=1}^{T} (x_t - y_t)\right]. \qquad (1.2a)$$

However, for many decision making situations, total expected discounted harvest may be a preferable criterion, since a discount factor can represent a measure of risk or uncertainty about the system, over and above the variability due to the random variable d. More formally, if α is a discount factor $0 \leq \alpha < 1$, the problem is to:

$$\text{maximize } E \left[\sum_{t=1}^{\infty} \alpha^{t-1} p(x_t - y_t)\right] \qquad (1.2b)$$

subject to $0 \leq y_t \leq x_t$; and Equation (1.1)

where p is a weighting factor, which could be 1 or could represent the average weight of the salmon harvested.

All the results in this paper are for expected discounted return with $\alpha = 0.97$. For $\alpha = 1$, Equation (1.2a) must be used, since Equation (1.2b) is infinite for most policies. The choice of $\alpha = 0.97$ is arbitrary, though numerical runs for α ranging from 0.95 to 1.00 produced no significant changes in the results. When actually implementing a model, a careful choice of α must be made, and the sensitivity of the results to changes in the value of α should be tested. It should be mentioned that $\alpha = 1$ is just as much a discount factor as any other value and implies certain temporal preferences and attitudes towards risk that may not adequately reflect the decision maker's preferences.

The shortcomings of Equation (1.1a) or (1.1b) should also be noted, such as no account is taken of ocean harvesting of the salmon, particularly by a foreign nation. This just reinforces the idea that the purpose of this analysis is not optimization per

se, but rather to provide the decision maker with added insight and reasonable first choices.

Defining the Model on a Discrete Grid

In order to make Equation (1.2) amenable to numerical methods, it is necessary to define both the state space and the action space on a discrete grid, and then to redefine the transition probabilities, etc., on this grid. Several authors (Fox 1973; Bertsekas 1976; Hinderer 1978; Waldmann 1978; Whitt 1978; Larraneta[2]) have suggested techniques to reduce MDP's to a grid and give bounds on the error due to the approximation. I have shown elsewhere (Mendelssohn[3]) that grid choice can have a significant effect on the analysis. An optimal policy and the value of an optimal policy may not be greatly affected by the choice of grid, but the estimated probabilistic behavior of the population dynamics is affected significantly by the choice of grid.

A first effort then is to find an adequate grid for the problem, a grid fine enough for both the desired accuracy and for realistic approximations of observed population sizes and coarse enough for computational efficiency. Increased computational efficiency makes it reasonable to solve many variations of a given model, which allows for a more thorough exploration of the management questions of interest and their sensitivity to key assumptions.

Several different grids were tried for Equation (1.2) for both the Branch and Wood Rivers.

To define Equation (1.2) on a given grid, suppose a grid of k points has been chosen on which to discretize the problem and assume, as is reasonable for this problem, that the reduced action space (how many spawners to leave) is equivalent to the state space (how many recruits are observed at the beginning of the period). From Equation (1.1), letting R_1 and R_2 represent the parameters of the Ricker equation

$$P(x_{t+1} \leqslant \omega | y_t) = P[(e^d) R_1 y_t \exp(-R_2 y_t) \leqslant \omega]$$

$$= P(d \leqslant \ln\omega - \ln a) \qquad (2.1)$$

where $a = [R_1 y_t \exp(-R_2 y_t)]$. Let Φ be the standard normal integral for a random variable $d = d/\sigma$, and let x_i, x_{i+1} be any two adjacent points on the grid. Then:

$$P(d \leqslant \ln x_i - \ln a) = \Phi\left(\frac{\ln x_i - \ln a}{\sigma}\right)$$

$$P(d \leqslant \ln x_{i+1} - \ln a) = \Phi\left(\frac{\ln x_{i+1} - \ln a}{\sigma}\right)$$

so that one method of defining the transition probabilities on a grid is:

$$P(x_{t+1} = x_{i+1} \mid y_t) = \Phi\left(\frac{\ln x_{i+1} - \ln a}{\sigma}\right) - \Phi\left(\frac{\ln x_i - \ln a}{\sigma}\right).$$

The discrete probability when the action is y_t is equal to the total probability of going to any state in the interval (x_i, x_{i+1}).

If zero is included as a state, the procedure needs to be modified slightly. Suppose the probability of going to x_1 is known for each decision y. Then an arbitrary fraction of this probability is assigned as going to the zero state. In this paper, one-half of the probability in the interval $(0, x_1)$ is assigned to the zero state. The results have been found not to be sensitive to the value of the fraction; this is because zero is an absorbing state. Either there exists a policy that never reaches $(0, x_1)$ and hence never reaches zero, or else with probability one the population goes to zero in finite time. Hence, it is the size of $(0, x_1)$ that most influences the results, not the fraction of this total that is assigned to going to the absorbing state.

Adding an absorbing state is sensible if the absorbing state is thought of as all states at low enough population levels such that it would take years for the fishery to recover again, if it recovers at all. Without the absorbing state, the models in Equation (1.1a, b) will always recover in fairly short order. Since fisheries can be depleted, the

[2]Larraneta, J. C. 1978. Approaches to approximate Markov decision processes. Paper presented at Joint National ORSA/TIMS Meeting, Nov. 13-15, 1978, Los Ang., Calif.

[3]Mendelssohn, R. 1978. The effects of grid size and approximation techniques on the solutions of Markov decision problems. SWFC Admin. Rep. 20H, 15 p. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv. NOAA, Honolulu, HI 96812.

inclusion of an absorbing state would seem to be a more realistic assumption. It is included in what follows.

A coarser grid implies, in a sense, less information about the state of the system. As the interval $(0, x_1)$ becomes large, our information has decreased about the true state of the population and this increased uncertainty is reflected in increased risk of absorbtion. Similarly, a finer grid implies more exact information—a grid should not be used which is finer than the precision of the estimate of the population size.

Optimal policies for grids of 16, 26, 51, 101, and 501 equally spaced points (including zero) for both rivers are shown in Table 1. The optimal equilibrium population for the equivalent deterministic models are shown also. All numbers are in units of millions of fish.

The optimal policies are all of the base stock variety, i.e. it is optimal to harvest to a fixed number of spawners, or else not to harvest at all. If the 501-point grid is taken as the standard, it can be seen that each coarser grid has as its base stock size the grid point closest to the base stock size for the 501-point grid.

Figure 1 gives the long-run (ergodic) cumulative distribution of being in any state when following an optimal policy on grids of 16, 26, 51, and 101 points. Grid size can be seen to play a crucial part in estimating the probabilistic behavior of the population. For the Wood River, extinction with probability one is predicted on grids of 16 and 26 points, while the probability is zero on grids of 51 and 101 points, so long as zero is not the initial state. Similar but not identical results are valid for the Branch River. It should be emphasized that for $\alpha = 1$, i.e., when the objective is given by Equation (1.2a), the estimated average per period harvest of any policy depends entirely on the ergodic distribution that arises from that policy. Therefore, this variation in estimated long-run behavior due to changes in grid size is nontrivial.

Probability one of extinction occurs because for a finite state, irreducible Markov chain with an absorbing state, the absorbing state is reached in finite time with probability one. However, for the larger grids, there exist policies that are reducible, in the sense that if the chain does not start in the interval $(0, x_1)$, it will never enter that interval. Since $P[x_t \epsilon (0, x_1)] = 0$, and a fraction of this probability has been assigned to the zero state, then $P(x_t = 0) = 0$. When using the smaller grids that induce Markov chains that are irreducible, the estimated time till absorption varies greatly also. For example, for the Branch River, if $P(x_1 = 0) = 0$ and $P(x_1 = \omega) = 1/(N-1)$, where ω is a grid point and N is the number of states, then a 16-point grid predicts absorption with probability one after 2,000 iterations, the 26-point grid predicts only a 76% chance of absorbtion after 2,000 iterations, and the 51-point grid predicts only a 17% chance of absorption.

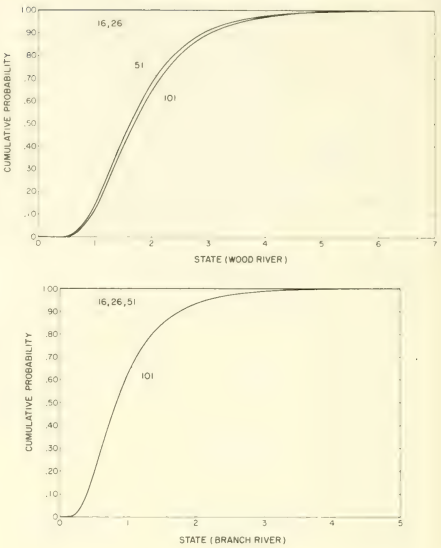


FIGURE 1.—Ergodic cumulative distributions for optimal harvesting strategies on grid sizes of 16, 26, 51, and 101 points for the Wood River and the Branch River.

When maximizing total expected discounted return, the discounted mean return depends on the values of these intermediate probability distributions, so that coarser grids can be expected to underestimate the long-run value of the harvest.

Finally, for the Wood River, note that the 51- and 101-point grids have similar long-run behavior. These results suggest that in order to find

TABLE 1.—Optimal policies for the different grid sizes.

Wood River	Grid size	Branch River
$y_t = \min(x_t, 0.9333)$	16	$y_t = \min(x_t, 0.3333)$
$y_t = \min(x_t, 0.840)$	26	$y_t = \min(x_t, 0.4000)$
$y_t = \min(x_t, 0.700)$	51	$y_t = \min(x_t, 0.3000)$
$y_t = \min(x_t, 0.770)$	101	$y_t = \min(x_t, 0.3500)$
$y_t = \min(x_t, 0.742)$	501	$y_t = \min(x_t, 0.3500)$
Equilibrium stock 0.735	Deterministic	Equilibrium stock 0.345

good policies, it is only necessary to use a grid size of 26 to 51 points for the problems under consideration. However, to analyze the long-run (probabilistic) behavior of a given policy, it is necessary to use a grid containing no fewer than 100 points.

It should be reemphasized that the reason for considering a coarser grid is that a smaller problem size allows for many problems to be solved at a small cost. This is desirable to obtain insight into the sensitivity of the problem. However, it is possible to solve quite large problems, making use of a variety of methods to accelerate computations (see for example Porteus 1971; Hastings and van Nunen 1977). For example, the 501-point grid for the Branch River used 1.80 s of CPU (central processing unit) time to perform the optimization. Computations, when smoothing costs are included (see Policy Analysis section), have 2,601 states. These used about 5 to 6 min of CPU time to perform the computations, but at a cost of about $20. Our experience is that it is possible to obtain reasonable estimates using coarse grids and that this suffices for initial policy investigation. However, it is worthwhile to reanalyze the final two or three problems of greatest interest on a finer grid.

POLICY ANALYSIS

For the Wood River, the optimal policy for Equation (1.2) is given by

$$y_t = \text{minimum}\,(0.770, x_t)$$

and it produces a mean per period harvest of 1.14758, and a standard deviation in the harvest of 0.8963. The median harvest is 0.91, and no harvest occurs roughly 4.3% of the time. A harvest of 25% or less of the mean harvest occurs roughly 15% of the time, while a harvest greater than the mean harvest occurs approximately 38% of the time.

Similarly, for the Branch River, an optimal policy for Equation (1.2) is given by

$$y_t = \text{minimum}\,(0.300, x_t)$$

and it produces a mean per period harvest of 0.6622, and a standard deviation in the harvest of 0.6120. The median harvest is roughly 0.500; there is a 3.9% chance of no harvest. A harvest of 25% of the mean harvest or less occurs roughly 14.5% of the time, and a harvest greater than the mean harvest occurs approximately 61% of the time.

While these policies are similar in form to policies that are optimal for a deterministic version of Equation (1.2), they differ greatly in the year-to-year dynamics. There are two ways of finding the optimal deterministic policy. The first way is to assume a general model of the form:

$$x_{t+1} = R_1 y_t \exp(-R_2 y_t)$$

The second method is to assume a general model of the form:

$$x_{t+1} = E \exp(d) R_1 y_t \exp(-R_2 y_t)$$

where as before, R_1 and R_2 are the parameters of the Ricker equation. The second method is preferable since it uses all the information available. As d is a normal random variable with mean zero and variance σ^2, it is easy to show that $\exp(d)$ is a lognormal random variable with expectation $\exp(\frac{1}{2}\sigma^2)$. Solving for the optimum sustained yield (OSY) population size for each river gives:

	Wood River	*Branch River*
x_{OSY}	0.735	0.345
OSY	1.11346	0.63804

Both OSY values are lower than the mean per period harvests in the stochastic models, but the variation is too high to allow this amount to be harvested each year. However, the x_{OSY} level is a good estimate of the base stock size, and it is known a priori from Mendelssohn and Sobel (in press) that a base stock policy is optimal.

In the deterministic model, once x_{OSY} is reached, both the population size and the harvest size are maintained at steady, equilibrium levels. An optimal policy for the stochastic model, however, produces large fluctuations in both and may allow no harvesting 1 yr out of 25 in the long run. For many fisheries, these "boom and bust" conditions may not be acceptable. Many people, especially those with interest or mortgage payments, as are many fishermen, are concerned about smoothness of income received as well as the total amount received. The final decision on the acceptable amount of fluctuation is, of course, up to the decision maker with appropriate input.

There are several methods available to try to find a balance between the smoothness of the random income stream and its total discounted expected value. Walters (1975) and Walters and Hilborn (1978) suggested fixing a given mean harvest

u, and then finding a policy that minimizes $\lim_{T\to\infty} E\frac{1}{T}\sum_{t=1}^{T}(z_t-u)^2$. This methodology depends on the values of u chosen. It also determines the policy that minimizes the approximate long-run variance for a given long-run mean harvest. This is not equivalent to reducing the size of the year-to-year fluctuations.

A second method is to include "smoothing costs" into the one-period return. This approach has been studied analytically by Mendelssohn.[4] Let γ be the cost of a unit decrease in the harvest from year to year, and let ϵ be the cost of a unit increase in the harvest from year to year.

If z was harvested last year, then net revenues this year, for any harvest z_t, are decreased by

$$\begin{cases} \gamma(z-z_t) & \text{if } z>z_t \\ 0 & z=z_t \\ \epsilon(z_t-z) & z<z_t \end{cases}.$$

Amended to Equation (1.2), this would imply a one-period net benefit of

$$p(x_t - y_t) - \gamma[z - (x_t - y_t)]^+ - \epsilon[(x_t - y_t) - z]^+$$

where $(a)^+$ denotes the positive part of a. An alternate form is to let $e = (\gamma-\epsilon)/2$ and $c = (\gamma+\epsilon)/2$. Then the one-period return is:

$$p(x_t - y_t) + e(x_t - y_t) - c\,|\,(x_t - y_t) - z\,| - ez.$$

One advantage to the smoothing cost approach over other approaches is that p, e, and c can be normalized so as to be interpreted as relative prices. That is, the normalized values $p = 1$, e/p, and c/p can be interpreted as the value of having the between period harvest "smoothed" by one unit relative to the value of one unit of additional harvest. Actual relative values are often difficult to determine. But by parameterizing on e and c, it is possible to present a decision maker not only a range of possible "optimal" policies and their consequences, but also some feeling for the relative trade off between total income and the smoothness of the received income stream.

For the Wood and Branch Rivers, two sets of computations were performed. The first set assumes that $\gamma = \epsilon$, i.e., there is an equal concern for increases in allowable harvest as well as for decreases. This is equivalent to $e = 0.0$ and $c = \gamma$ (or equivalently ϵ). The motivation for this cost structure is that fishermen typically resist any decrease in the allowed harvest, hence $\gamma>0$. However, allowing increases in the harvest size often signals fishermen to gear up and invest in equipment, thereby making it even more difficult to decrease the allowable harvest later on. Therefore this cost should be equal to a cost due to a decrease in the harvest.

As a counterbalance to this, a second set of computations were performed with $\gamma>0$ but $\epsilon = 0$, i.e., a cost only if the harvest is decreased. This is equivalent to $c = e = \gamma/2$.

For the first set of computations, with $e = 0.0$ and $p = 1.0$, values of c of 0.25, 0.50, 0.75, 1.00, 1.25, 1.50, 1.75, and 2.00 were used. These are equivalent to relative values of ⅛, ¼, ⅜, ½, ⅝, ¾, ⅞, and 1. For the second set of runs, with $c = e$, and $p = 1.0$, values of 0.25, 0.50, 0.75, 1.00 and 1.25 were used. These are equivalent to a ratio of γ/p equal to ¼, ½, ¾, 1, 1¼. The results are summarized in Figure 2(a)-(m) and Figure 3(a)-(m), which show an optimal policy for each river for each of these cases. All computations were performed on 26-point grids.

The figures are read as follows. Suppose z was harvested last year and x is the observed population size this period. Find the point (x, z) on the graph and follow the arrow in that zone to the appropriate boundary as indicated. Then read off the z value of this point; this is the optimal amount to harvest during this period.

For example, if $c = 0.50$, $e = 0.00$, $x_t = 0.84$, and the harvest last period was 0.28, Figure 2(b) shows that the optimal policy for the Wood River is to harvest 0.28 this period. Note that the dashed line is the equivalent base stock harvest with no smoothing costs.

While the policies in Figures 2 and 3 are optimal for the given relative values of p, e, and c, they are complex in nature and would be difficult for a layperson to understand. Practical management often implies determining simpler, good but suboptimal policies that achieve the same objectives. These policies are often more desirable since they

[4]Mendelssohn, R. 1976. Harvesting with smoothing costs. SWFC Admin. Rep. 9H, 26 p. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96812.

are easier to implement and easier to explain the rationale to the public.

As an example of suboptimal, approximate policies, the following nine modified base stock policies were examined:

Wood River

1) Base stock policy, base stock size = 0.84.
2) Policy of base stock size of 0.56 till 2.52, then a base stock size of 0.84.
3) Policy of base stock size of 0.56 till 1.40, then a base stock size of 0.84.
4) Harvest 0 till 0.28, harvest 0.28 till 0.84, a base stock size of 0.56 till 2.52, then a base stock size of 0.84.

Branch River

5) Base stock policy, base stock size of 0.40.
6) Base stock size of 0.4 till 1.6, then a base stock size of 0.6.

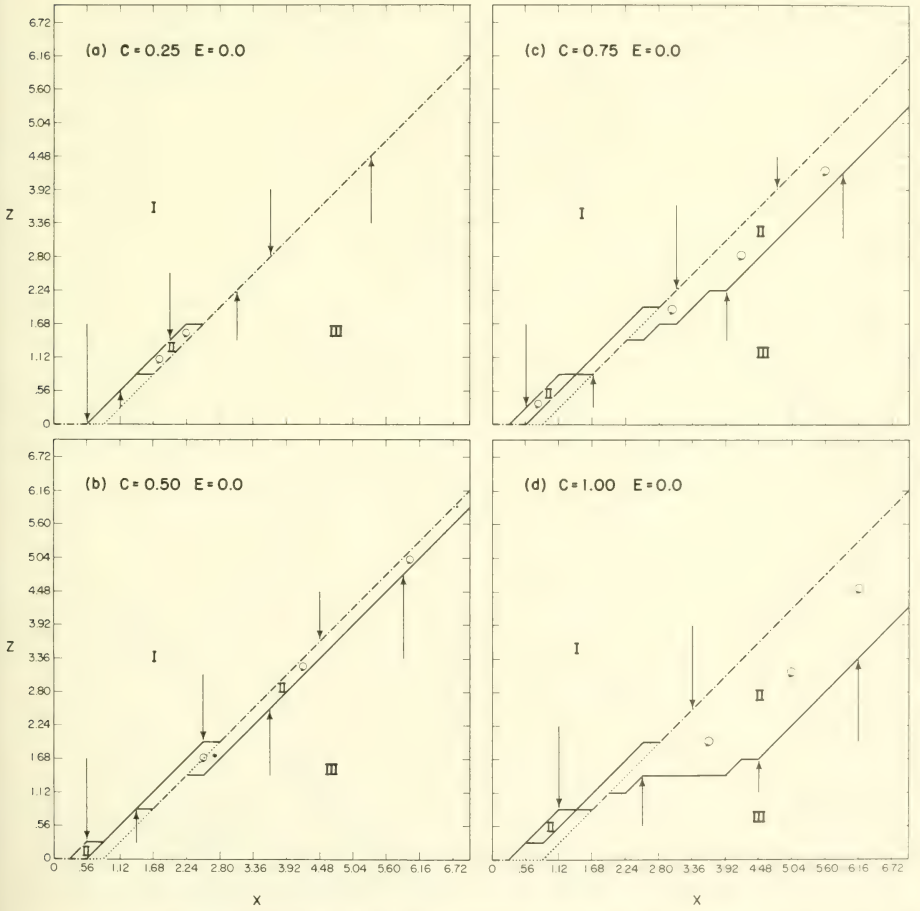


FIGURE 2(a-m).—Optimal policy functions for the Wood River for various assumptions about the relative value of smoothing costs. (See text for details).

7) Base stock size of 0.2 till 0.6, then a base stock size of 0.4.
8) Base stock size of 0.2 till 1.0, then a base stock size of 0.4.
9) Base stock size of 0.2 till 0.4, base stock size of 0.4 till 1.2, base stock size of 0.6 after that.

These nine approximate policies were devised by examining the functions that define the three regions in Figures 2 and 3. These approximate the boundaries of the three regions where the smoothing costs are one-fourth to one-half the per unit value of the harvest. The mean per period harvest, variance, standard deviation, median per period harvest, etc. for these nine policies are given in Table 2.

Policies 3 and 4 for the Wood River and 8 and 9 for the Branch River demonstrate how these approximate policies tend toward smoothing policies. For example, policy 4 has the same median harvest as the optimal base stock harvest, almost never closes the fishery, significantly de-

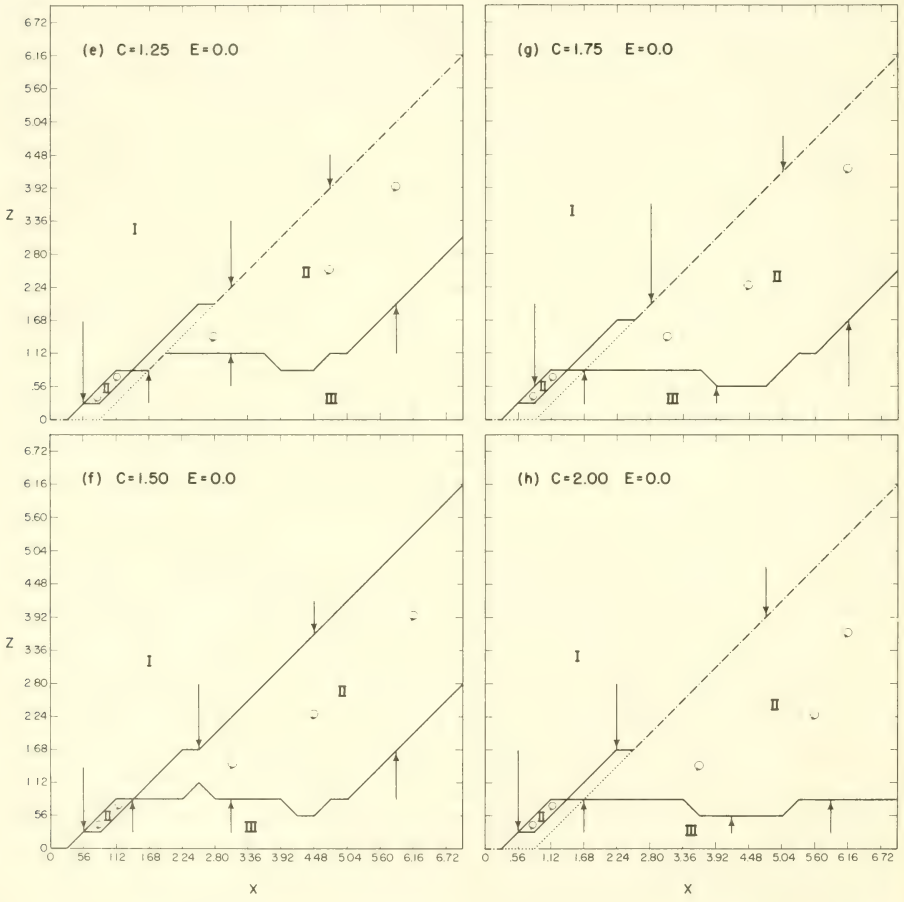


FIGURE 2.—Continued.

creases the percent of time there are low catches, and only reduces the mean per period harvest by 33,800 fish. In order to achieve a smoother catch, "potlatch" harvests from time to time have been sacrificed.

When looked at closely, these policies are actually very intuitive and represent an interesting variant of a base stock policy. These policies replace a single base stock size by a dual base stock size policy. The first base stock size is lower than the original one, while the second base stock size is greater than or equal to the original base stock size. This means that there are fewer states where there is no harvesting, but also lowers the likelihood of the really big harvests. The mean per period harvest tends to be very sensitive to these big harvests, while the median is not, particularly since the very large harvests are not too frequent.

It is curious that the population dynamics are so sensitive to such fine tuning, for the difference between policy 1 and policy 3, say, is quite marginal. It would be an interesting area of future

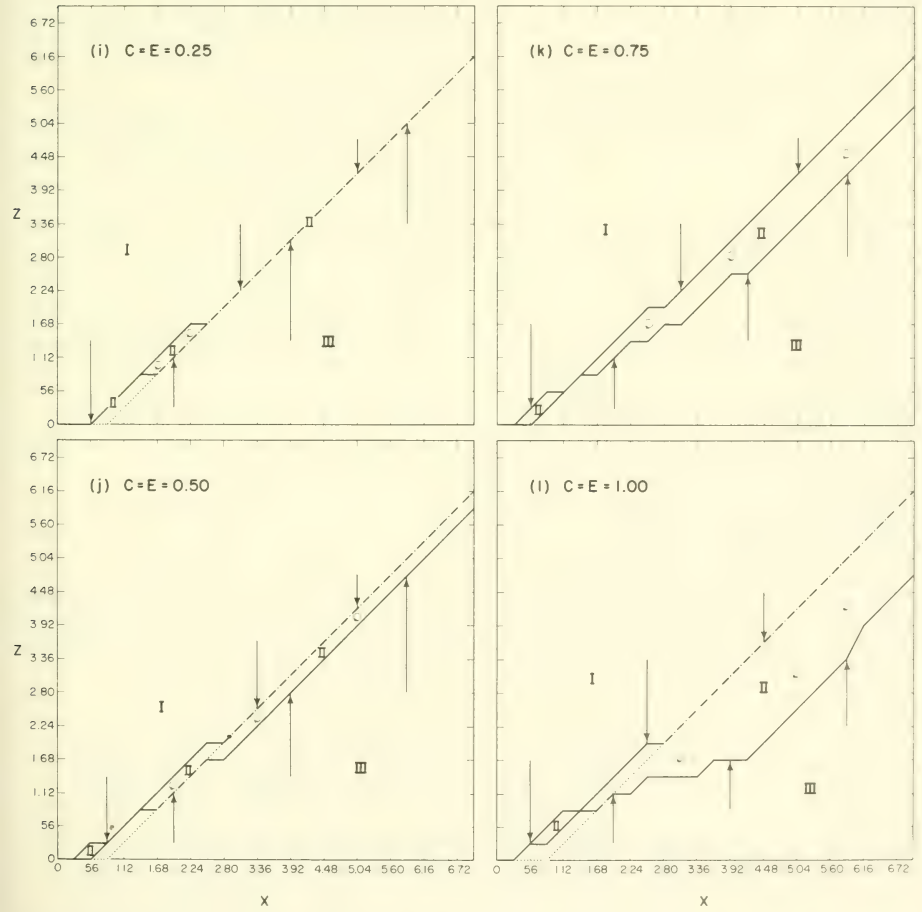


FIGURE 2.—Continued.

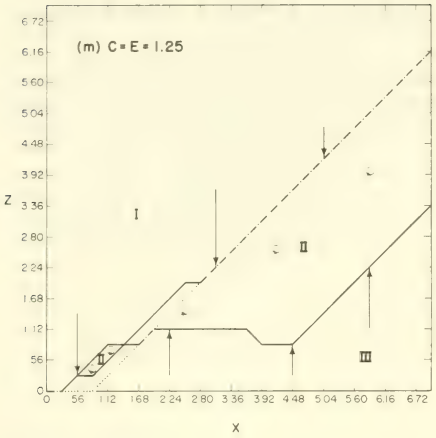


FIGURE 2.—Continued.

research to determine guidelines for when fine tuning would be expected to produce such "trimming" of the tails of the ergodic (long-run probability) distribution.

Including smoothing costs also tells us a great deal about traditional concepts of fisheries management, such as MSY. It is clear from Figures 2 and 3 that anything close to an MSY policy is optimal only if the smoothing costs exceed the per unit value of the harvest. As whole systems of laws for regulating fisheries have been constructed around the idea of smooth, constant harvests, it is clear that this imputes lower average catches, and a significant preference for constancy of the harvest over total amount harvested.

The analysis has assumed that Equation (1.1) or similar equations are available, and that the parameter estimates are accurate (in this case, estimates of R_1, R_2, and σ^2). In the latter case, management measures would seem more reasonable if they were known to be robust against misspecifying the parameters. This involves knowing how an optimal policy and total expected value would vary if the true underlying parameter values differ from those specified, and also how the estimate of the long-run probability distribution differs from the true one.

Walters and Hilborn (1976) have examined a similar question of trying to solve the Bayes model of this problem, i.e., where there is an original prior probability given to each value of the parameter, and this probability is updated each period using Bayes theorem and the observed values during the period. However, they could not obtain a solution, and Walters and Hilborn (1978) raised questions as to the validity of some of their numerical approximations.

Fortunately, qualitative results are possible for this particular class of Bayes problems. Let Θ be the parameter (or vector of parameters) under consideration. Let $q_0(\Theta)$ be the initial prior distribution on Θ, and let $q_n(\Theta)$ be the updated prior distribution after n period has elapsed. Let Ω be the set of all possible prior distributions. Then it is proven in van Hee (1977a) that if the state of the system is expanded to (x_t, q_t), the resulting optimization problem is Markovian. Following arguments similar to those in Scarf (1959) and van Hee (1977a) it follows that an optimal Bayes policy takes the form:

For each element $q \in \Omega$, there is an $x(q)$ such that:

$$\text{do not harvest if } x_t \leq x(q)$$

$$\text{harvest } x_t - x(q) \text{ if } x_t > x(q).$$

For example, if σ^2 in the distribution of d is itself a random variable, then each possible probability distribution of σ^2 yields a possibly unique base stock size policy.

TABLE 2.—Vital statistics for the nine policies approximating the smoothing cost policies for Wood and Branch Rivers.

River	Policy	Mean per period harvest	Variance of per period harvest	Standard deviation	% time no catch	% time less than 25% of mean	% time greater than mean catch	Median catch	Relative value: smoothing/price
Wood	1	1.1357	0.8468	0.9202	5.6	16.8	39	0.98	0/1
	2	1.0993	0.5460	0.7389	1.7	10.7	39.8	0.98	1/8
	3	1.1203	0.6506	0.8066	1.1	7.7	43.2	0.91	1/4
	4	1.1019	0.5758	0.7588	0.02	10.47	40	0.98	1/2
Branch	5	0.6528	0.3982	0.6310	9.2	21.8	40	0.500	0/1
	6	0.6290	02532	0.5032	9.1	21.5	37.2	0.500	1/4
	7	0.6272	0.3077	0.5547	1.2	27.7	31.3	0.400	1/2
	8	0.5920	0.2202	0.4693	1.9	35.7	26.3	0.500	3/8
	9	0.5995	0.3038	0.5512	0 72	22.83	39.3	0.500	3/4

Van Hee (1977a) defined a set of policies that he terms Bayes equivalent policies. For problems such as the salmon models under discussion, a Bayes equivalent policy would be found as follows:

1) At the start of the period, the prior probability distribution is $q(\Theta)$.

2) The expected transition function (expectation with respect to Θ) is calculated, i.e.,

$$p(d, q) = \int p(d \mid \Theta) q(d\Theta) \qquad (4.1)$$

where $p(\cdot \mid \cdot)$ describes the dependence of the random variable d on Θ.

3) $p(d, q)$ is used to solve a non-Bayesian Markov decision process, with $p(d, q)$ as the transition function.

4) The optimal policy from step 3 above is used for one period.

5) $q(\Theta)$ is updated using Bayes theorem and the observations from the last period, and the updated $q(\cdot)$ is used in step 1 at the next time period.

It is worth noting that a Bayes eqivalent policy

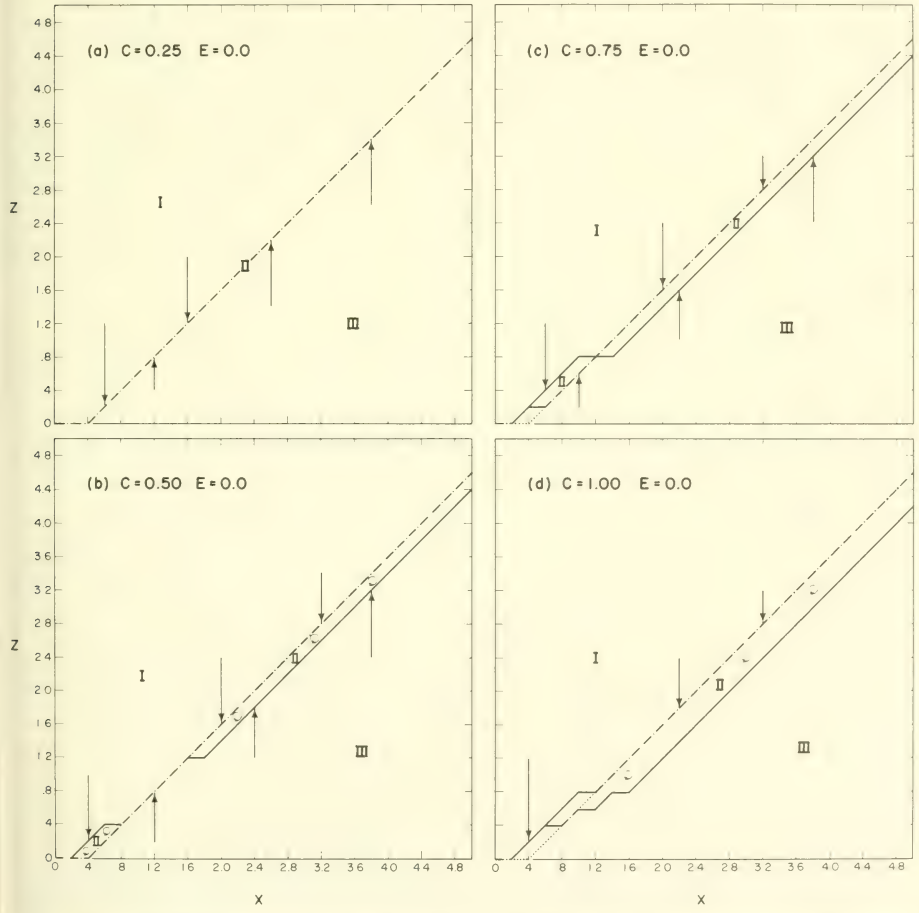


FIGURE 3(a-m).—Optimal policy functions for the Branch River for various assumptions about the relative value of smoothing costs. (See text for details.)

is adaptive, as the prior distribution is updated each period. Moreover, it is not the same as fixing Θ at its estimated value, and using a fixed value of Θ in step 3. The difference can be seen in the integral in Equation (4.1). The reason for considering Bayes equivalent policies is that van Hee (1977a, theorem 3.1) proved that for the models under discussion, when the objective is given by Equation (1.2a) or (1.2b), then the Bayes equivalent policy is optimal for the full Bayes model. For example, in Walters and Hilborn (1976), the parameter Θ is a scalar, i.e., R_2 in our notation. Their problem, for which an optimal policy was not found, can be solved by following a policy outlined in the five steps above.

Many models will not have the necessary structure for a Bayes equivalent policy to be optimal for the full Bayes model, and unlike salmon management, estimates of the population size may not be available every year. A legitimate question is: suppose the present best estimate of Θ were to be used from hereafter. What would be the loss in

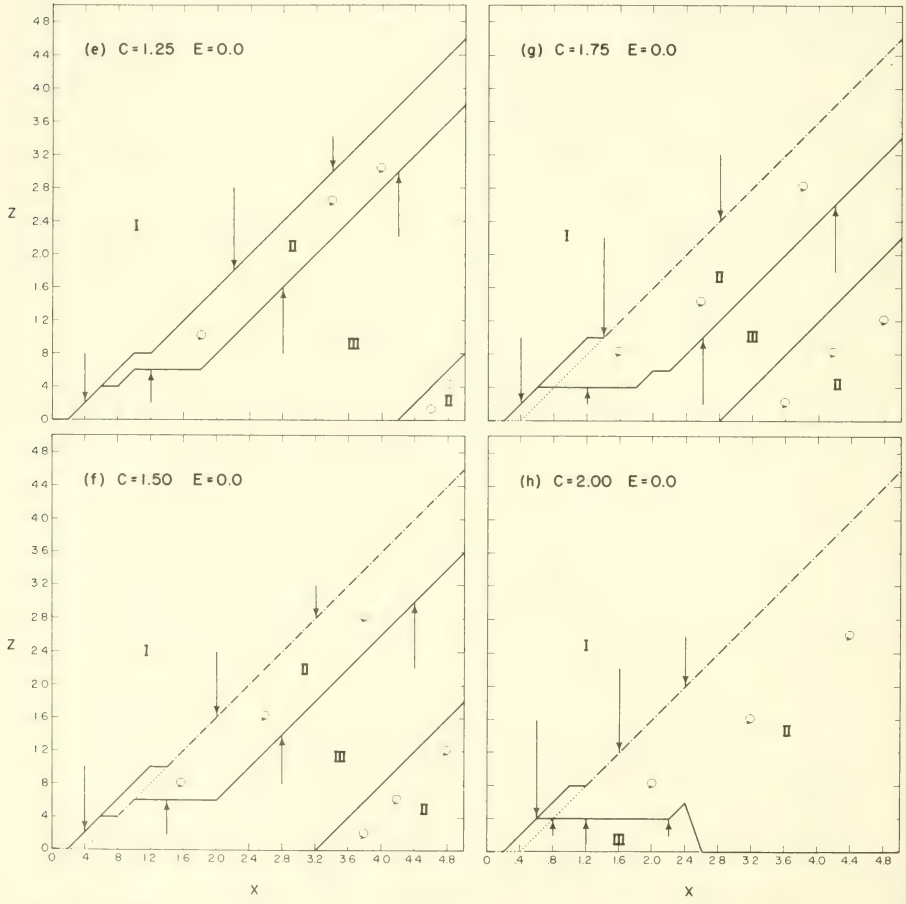


FIGURE 3.—Continued.

expected value? Van Hee (1977b) gave bounds on this expected loss that are easy to compute. To obtain a feel for these bounds, both σ^2 and R_2 are assumed to be random variables. For the Wood River, R_2 could take on the values -0.6, -0.8 and -1.0, and for the Branch River R_2 could take on the values -1.5, -1.85, and -2.00. For the Wood River, σ^2 could assume the values of 0.35, 0.45, and 0.55, and for the Branch River σ^2 could assume the values 0.48, 0.58, and 0.68. Three probability distributions were used as the present prior probability of the parameter values. These were (⅓, ⅓, ⅓,), (¼, ½, ¼), (⅛, ¾, ⅛). The results of the optimization using the parameters at each fixed value (which are needed to calculate the bounds) are given in Table 3. Table 4 gives the bounds on the expected loss of value from using the present estimates of the parameters as in Equation (1.1).

Table 3 suggests that as σ^2 varies for fixed values of R_1, R_2, the mean per period harvest varies little, but the variance of the long-term harvest size distribution increases significantly. As R_2

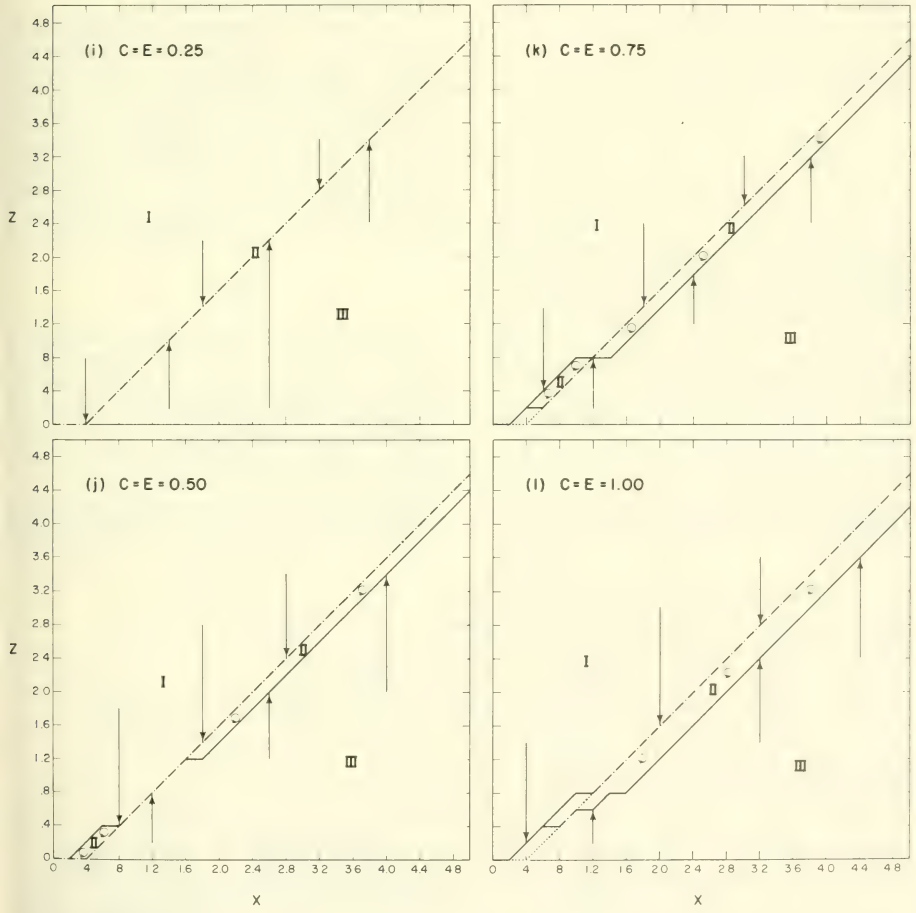


FIGURE 3.—Continued.

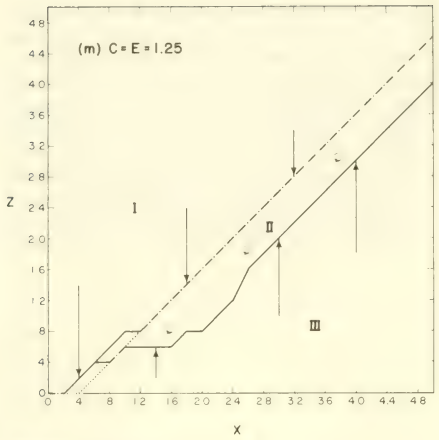


FIGURE 3.—Continued.

varies for fixed values of R_1, σ^2, both the mean and the variance vary significantly. Table 4 reinforces this impression to a degree. If the mean per period harvest does not vary significantly with changes in the value of σ^2, it might be expected that the present estimate of σ^2 will suffice. This is borne out by Table 4, where the bounds on the maximum expected total loss is <0.01, which is $<1\%$ of the optimal Bayes expected value.

Some significant expected loss in value when R_2 varies is seen, but the loss is less than might be expected from Table 3. The values in Table 4 when R_2 varies are all $<4\%$ of the true value. These results suggest that if Equation (1.1) is the correct form of the model, and the present parameter estimates have relatively small variance, then little is gained in expected value if the more complicated policy is used. The same may not be true if the population size is unobserved.

All of these results suggest a model that is fairly robust to our lack of understanding of nature. A possible explanation for this can be made from the discussion on the effect of grid size. As long as there is some cutoff population size below which no harvesting is allowed, and this cutoff assures that the absorbing state cannot be reached with probability one, then our management can only damage the stocks to a degree.

All of the policies examined in this paper have such a minimum cutoff. The rest of the policy will determine the relative mean and variance of the harvest, and techniques are presented to examine these features in detail. Uncertainty about the values of the parameters will affect the total return, but present estimates often can give a satisfactory approximation. The truly risk adverse decision maker can use present estimates of the parameters that are weighted to be on the cautious side.

SUMMARY

Uncertainty in fisheries management can be faced head on. Techniques exist that allow us to gain much insight on managing randomly varying populations. Optimization procedures allow us to reduce our attention to the few best policies, and to analyze their properties, rather than to pick policies ad hoc that meet no special criteria.

Optimization under uncertainty can also lead to a reconsideration of what is valued in managing a

TABLE 3.—Trials with varied parameters.

River	Value of R_2	Value of σr	Optimal policy	Mean per period harvest	Variance	% time no harvest
Wood	-0.800	0.35	min (x_t, 0.7)	1.0680	0.390976	0.79
Wood	-0.800	0.55	min (x_t, 0.77)	1.2267	1.2422	7.8
Wood	-0.600	0.458	min (x_t, 0.980)	1.5108	1.3136	3.8
Wood	-1.000	0.458	min (x_t, 0.560)	0.9225	0.4839	3.29
Branch	-1.845	0.48	min (x_t, 0.35)	0.6122	0.2253	3.54
Branch	-1.845	0.68	min (x_t, 0.35)	—	—	—
Branch	-1.500	0.579	min (x_t, 0.40)	1.989	0.5254	5.82
Branch	-2.000	0.579	min (x_t, 0.30)	0.9075	0.3068	5.82

TABLE 4.—Largest possible deviation in value of the approximate policy compared with the true Bayes policy.

Probability distribution	When R_2 is uncertain			When σ is uncertain		
	$\frac{1}{3}, \frac{1}{3}, \frac{1}{3}$	$\frac{1}{4}, \frac{1}{2}, \frac{1}{4}$	$\frac{1}{8}, \frac{3}{4}, \frac{1}{8}$	$\frac{1}{3}, \frac{1}{3}, \frac{1}{3}$	$\frac{1}{4}, \frac{1}{2}, \frac{1}{4}$	$\frac{1}{8}, \frac{3}{4}, \frac{1}{8}$
Wood River	1.4	0.51	0.5	0.04	0.03	0.03
Branch River	1.04	0.47	0.38	0.01	≤ 0.01	≤ 0.01

fishery—in the examples considered, some consistency in the amount harvested is a desirable alternative to high year-to-year fluctuations in the harvest size. But this reduced the average per period catch. Only in extreme situations, where the cost of smoothing out the catch is greater than the unit value of the catch, does any policy resembling MSY become optimal.

Finally, it is possible to obtain an understanding of how robust the management measures are to misspecifications of the underlying model. This is important, since the model is only a guide to our decision making, not the answer. In the models considered, the "best" policies are robust in view of this uncertainty.

A question not examined is the assumption that the population size is observed at the start of each period. This too is usually costly, and inexact. Recently, I and E. J. Sondik developed an efficient algorithm that addresses the relative merits of different sampling intervals for obtaining population estimates.[5] Together, all of these techniques allow for an integrated, realistic approach to management under uncertainty.

ACKNOWLEDGMENTS

Debra Chow provided invaluable assistance in programming the computer runs. David Stoutemeyer of the University of Hawaii gave much useful advice on maximizing the efficiency of the optimization algorithm used. Lee Anderson, George Fishman, and Adi Ben-Israel gave important comments for improving an earlier version of this paper. The paper also benefited greatly from the comments of one of the referees and from C. Walters who tempered some remarks in a previous version.

LITERATURE CITED

ANDERSON, L. G.
1977. The economics of fisheries management. The Johns Hopkins Univ. Press, Baltimore, 214 p.

BERTSEKAS, D. P.
1976. Dynamic programming and stochastic control. Acad. Press, N.Y., 396 p.

CLARK, C. W.
1976. Mathematical bioeconomics: The optimal management of renewable resources. John Wiley and Sons, N.Y., 352 p.

FOX, B. L.
1973. Discretizing dynamic programs. J. Optim. Theory Appl. 11:228-234.

FOX, W. W., JR.
1970. An exponential surplus-yield model for optimizing exploited fish populations. Trans. Am. Fish. Soc. 99:80-88.
1971. Random variability and parameter estimation for the generalized production model. Fish. Bull., U.S. 69:569-580.
1975. Fitting the generalized stock production model by least-squares and equilibrium approximation. Fish. Bull., U.S. 73:23-37.

HASTINGS, N. A. J., AND J. A. E. E. VAN NUNEN.
1977. The action elimination algorithm for Markov decision processes. *In* H. C. Tijms and J. Wessels (editors), Markov decision theory, p. 161-170. Proceedings of the Advanced Seminar on Markov Decision Theory held at Amsterdam, the Netherlands, September 13-17, 1976. Mathematical Centre Tract 93. Mathematisch Centrum, Amsterdam.

HINDERER, K.
1978. On approximate solution of finite-stage dynamic program. Universität Karlsruhe, Fukultät für Mathematik, Bericht 8, 42 p.

MATHEWS, S. B.
1967. The economic consequences of forecasting sockeye salmon (*Oncorhynchus nerka*, Walbaum), runs to Bristol Bay, Alaska: A computer simulation study of the potential benefits to a salmon canning industry from accurate forecasts of the runs. Ph.D. Thesis, Univ. Washington, Seattle, 225 p.

MENDELSSOHN, R., AND M. J. SOBEL.
In press. Capital accumulation and the optimization of renewable resource models. J. Econ. Theory.

PELLA, J. J., AND P. K. TOMLINSON.
1969. A generalized stock production model. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm., Bull. 13:419-496.

PORTEUS, E. L.
1971. Some bounds for discounted sequential decision processes. Manage. Sci. 18:7-11.

REED, W. J.
1974. A stochastic model for the economic management of a renewable animal resource. Math. Biosci. 22:313-337.

RICKER, W. E.
1958. Maximum sustained yields from fluctuating environments and mixed stocks. J. Fish. Res. Board Can. 15:991-1006.

SCARF, H.
1959. Bayes solutions of the statistical inventory problem. Ann. Math. Stat. 30:490-508.

SCHAEFER, M. B.
1954. Some aspects of the dynamics of populations important to the management of the commercial marine fisheries. Inter-Am. Trop. Tuna Comm., Bull. 1:25-56.

VAN HEE, K. M.
1977a. Adaptive control of specially structured Markov chains. *In* M. Schäl (editor), Dynamische optimierung, p. 99-116. Bonner Mathematische Schriften 98, Bonn.
1977b. Approximations in Bayesian controlled Markov chains. *In* H. C. Tijms and J. Wessels (editors), Markov

[5]Mendelssohn, R., and E. J. Sondik. 1979. The cost of information seeking in the optimal management of random renewable resources. SWFC Admin. Rep. H-79-12, 15 p. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96812.

decision theory, p. 171-182. Proceedings of the Advanced Seminar on Markov Decision Theory held at Amsterdam, the Netherlands, September 13-17, 1976. Mathematical Centre Tract 93. Mathematisch Centrum, Amsterdam.

WALDMANN, K.-H.
1978. On approximation of dynamic programs. Preprint No. 439, Fachberech Mathematik, Technische Hochschule Darmstadt, 17 p.

WALTERS, C. J.
1975. Optimal harvest strategies for salmon in relation to environmental variability and uncertain production parameters. J. Fish. Res. Board Can. 32:1777-1784.

WALTERS, C. J., AND R. HILBORN.
1976. Adaptive control of fishing systems. J. Fish. Res. Board. Can. 33:145-159.
1978. Ecological optimization and adaptive management. Annu. Rev. Ecol. Syst. 9:157-188.

WHITT, W.
1978. Approximations of dynamic programs, I. Math. Oper. Res. 3:231-243.

ORGANOCHLORINE RESIDUES IN FISHES FROM THE NORTHWEST ATLANTIC OCEAN AND GULF OF MEXICO

VIRGINIA F. STOUT[1]

ABSTRACT

Residues of ΣDDT (*p,p'*-DDT and its metabolites *p,p'*-TDE and *p,p'*-DDE), PCB (polychlorinated biphenyls), dieldrin, and endrin were determined in the flesh of 700 specimens of fishes caught between 1973 and 1975 in the northwestern Atlantic Ocean and northern Gulf of Mexico off the coasts of the southeastern United States. Species with lowest oil content (<3%)—gag, *Mycteroperca microlepis*; black grouper, *M. bonaci*; red grouper, *Epinephelus morio*; and red snapper, *Lutjanus campechanus*—contained the least amounts of chlorinated hydrocarbon residues. Species with higher oil content—king mackerel, *Scomberomorus cavalla*, (3.5%) and Spanish mackerel, *S. maculatus*, (4.6%)—more consistently contained residues, but still at low levels. Significant correlations ($P<0.05$) were found in red snapper and king mackerel between lipid and size and between lipid and chlorinated hydrocarbon content. The correlations between lipid and PCB in gag and between lipid and DDT in black grouper were also significant. The highest mean values for any species were 0.18 ppm ΣDDT, 0.32 ppm PCB, 0.007 ppm dieldrin, and 0.008 ppm endrin. The highest level in any one composite sample of 10 fish was 1.0 ppm ΣDDT, 1.8 ppm PCB, 0.026 ppm dieldrin, and 0.026 ppm endrin.

Half a century ago manufacturers of surface coatings and of electrical equipment found a common interest in a newly introduced group of organochlorine chemicals, the PCB.[2] These compounds dissolve the inks in carbonless carbon paper, which duplicates without the use of carbon paper. They plasticize the waterproof coatings for dairy silos and fish tanks, and marine antifouling paint. The thermal and electrical properties of PCB are highly desirable in dielectric fluids, the electrical insulators in transformers and capacitors. The PCB are also highly resistant to chemical and biological degradation, and these properties, too, are valued by industrial users.

Immediately following World War II, another organochlorine chemical, DDT, became the magic tool of the medical profession, deeply concerned with preventing outbreaks of infectious, insect-borne diseases. Enormous quantities of DDT were used to prevent epidemics of typhus and plague in war-torn Europe. DDT was dramatically effective in controlling lice and fleas, which carried these diseases. The use of this and related compounds spread rapidly for mosquito and agricultural pest control. Before insect resistance developed, DDT reduced the incidence of malaria to a very low level.

Since PCB and the organochlorine pesticides are not only stable but also easily dispersed in the air and through the water, it is not surprising in retrospect that they are now found even in the polar regions (Sladen et al. 1966; Risebrough et al. 1976; Bowes and Jonkel 1975) and that chlorinated hydrocarbon pollution has become a worldwide problem. Not until the 1960's did appreciation of the adverse effects of these chlorinated hydrocarbons begin to develop. "Silent Spring" (Carson 1962) described the effects on the environment of the accumulation of DDT, and Jensen (Anonymous 1966; Jensen et al. 1969) found PCB in marine animals. Burdick et al. (1964) noted reproductive failure in lake trout when the eggs contained a high level of ΣDDT. Aulerich et al. (1973) traced the reproductive failure and mortality in ranch-grown mink back to coho salmon, *Oncorhynchus kisutch*, from Lake Michigan and ultimately to the PCB they contained. Only recently fin erosion, a disease associated with municipal and industrial discharges, was related to ΣDDT (Mearns and Sherwood 1977). Montrose Chemical Company released wastes from DDT manufacture directly into

[1]Northwest and Alaska Fisheries Center Utilization Research Division, National Marine Fisheries Service, NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112.

[2]Abbreviations used in this manuscript: DDE = *p,p'*-dichlorodiphenyldichloroethylene; DDMU = *p,p'*-dichlorodiphenylchloroethylene; DDT = *p,p'*-dichlorodiphenyltrichloroethane; PCB = polychlorinated biphenyls; Σ DDT = DDT and its metabolites DDE and TDE; TDE = *p,p'*-dichlorodiphenyldichloroethane.

Manuscript accepted August 1979.
FISHERY BULLETIN: VOL. 78, NO. 1, 1980.

the Los Angeles County sewer system which flows via sewer outfalls into the marine environment of southern California. From this unanticipated source of ΣDDT pollution, high levels of ΣDDT developed throughout the southern California marine environment from mollusks (Young et al. 1976), crustaceans (Burnett 1971), and fishes (McDermott-Ehrlich et al. 1978) to marine birds (Anderson et al. 1975) and cetaceans (Le Boeuf and Bonnell 1971). Henderson et al. (1969, 1971) found organochlorine residues in freshwater fishes throughout the United States. Some species of freshwater fishes, especially those from the Great Lakes, contained levels of chlorinated hydrocarbons that exceeded the U.S. Food and Drug Administration guidelines (Reinert 1970; Veith 1975). In recent years, the use of chlorinated hydrocarbons has been drastically curtailed, but concern remains about the continuing occurrence of these toxic compounds in the marine environment.

Fishes and shellfishes are excellent organisms for monitoring chlorinated hydrocarbons. Shellfishes have been used as indicators of short-term pollution (Butler 1973; Goldberg et al. 1978) because they accumulate and depurate these substances readily. Fishes, on the other hand, reflect long-term exposure since they lose chlorinated hydrocarbons slowly, if at all (Lieb et al. 1974). Butler and Schutzmann (1978) have reported on pesticides and PCB in yearling estuarine fishes of the United States. Outside of their study, however, few data on fishes for human consumption from the western Atlantic Ocean have been published except on fishes from Canadian waters (Sims et al. 1977). The study reported here was undertaken to obtain information about levels of ΣDDT, PCB, dieldrin, and endrin in fillets from fishes caught in the northwestern Atlantic Ocean and northern Gulf of Mexico. Six marine species of both commercial and sport value have been examined.

METHODS

Samples of gag, *Mycteroperca microlepis*; black grouper, *M. bonaci*; red grouper, *Epinephelus morio*; red snapper, *Lutjanus campechanus*; king mackerel, *Scomberomorus cavalla*; and Spanish mackerel, *S. maculatus*, were collected from the northwestern Atlantic Ocean and northern Gulf of Mexico, from Beaufort, N.C., south to the Florida Keys, and west to Aransas Pass, Tex. Sampling occurred between October 1973 and October 1975, but mainly in 1975. Specimens were frozen and held at −18° C. They were thawed for filleting, grinding, compositing, and refrozen until analysis. In the aggregate, 70 samples each containing 10 fish of the same species and of similar size were obtained. Each sample was a composite of equal weights of ground skinless fillets from the 10 individual fish. At most sites, two or three samples from different size fish were selected. The collection sites, size, and lipid content of the specimens are listed in Table 1.

Extracts were prepared by the procedures of Reinert (1970). Samples for ΣDDT and PCB analysis were extracted with propanol-2/benzene (1:1), and the extracted materials transferred to hexane by repeated codistillation of the propanol-2, benzene, and water with hexane. One aliquot of the hexane extract was evaporated to minimum weight for determination of the lipid content. Another aliquot was cleaned up on Florisil.[3] PCB were separated from TDE, DDT, and most of the DDE on activated silica gel (Snyder and Reinert 1971), which also separates the interfering hydrocarbons, phenanthrene, fluoranthrene, and pyrene from the PCB (Zitko 1978). At least 90% of the PCB was contained in the pentane fraction, which also contained part of

[3]Mention of specific products or companies in this paper does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Collection sites, size, and lipid content of fishes from the northwest Atlantic Ocean and Gulf of Mexico.

Species	Sites[1]	No.[2]	Fork length (cm)		Weight (kg)		Lipid content (%)	
			Mean	Range[3]	Mean	Range[3]	Mean	Range[3]
Gag	1, 2, 3	8	86	64-108	9.77	3.79-18.32	2.9	0.2-5.9
Black grouper	5, 6	6	77	54- 96	7.01	1.98-12.70	0.6	0.2-1.2
Red grouper	1, 4, 5, 6	10	68	52- 82	6.08	2.42-11.50	0.5	0.1-1.0
Red snapper	1, 2, 3, 4, 5, 6, 7, 8	18	65	45- 83	5.94	1.65-11.35	1.5	0.4-3.9
King mackerel	1, 2, 3, 4, 5, 6, 9	18	87	55-119	6.01	1.20-12.91	3.5	0.4-7.5
Spanish mackerel	3, 4, 5, 6, 7	10	54	45- 64	1.41	0.48- 2.34	4.6	1.7-9.4

[1]1 - Beaufort, N.C.; 2 - Savannah, Ga.; 3 - Florida, East Coast; 4 - Florida Keys; 5 - Tampa/St. Petersburg, Fla.; 6 - Panama City, Fla.; 7 - Mobile, Ala.; 8 - Pascagoula, Miss.; 9 - Aransas Pass, Tex.
[2]Number of composites, each consisting of 10 fish.
[3]Range of means of individual composites.

the DDE. All of the TDE and DDT eluted into the benzene fraction. For dieldrin and endrin analysis, tissues were saponified with KOH in aqueous ethanol, extracted with hexane, and cleaned up on Florisil. Since the specimens, originally collected for trace-metal analysis, were stored in polypropylene containers (Falcon No. 4014) with polyethylene lids (Falcon No. 4017), the containers and lids were also analyzed to assure freedom from interfering substances. The details of our procedures were published previously (Stout and Beezhold 1979). Blanks carried through the whole procedure for either PCB and ΣDDT or dieldrin and endrin showed no chromatographic peaks which interfered with quantitation of the chlorinated hydrocarbons.

The extracts of the fishes were quantitated by electron-capture gas chromatography. A Varian 600 C gas chromatograph with a titanium tritide detector was fitted with a 1.5 m (5 ft) × 0.32 cm (0.125 in) o.d. glass column containing a mixture of equal parts of 15% QF-1 on 80-100 mesh Gas Chrom Q and 10% DC-200 on the same support (Burke and Holswade 1966). Reference standards of *p,p'*-DDE, *p,p'*-DDMU, *p,p'*-TDE, *p,p'*-DDT, dieldrin, and endrin were obtained from the U.S. Environmental Protection Agency, Health Effects Research Laboratory, Research Triangle Park, N.C. Aroclor 1254 obtained from the Monsanto Company, St. Louis, Mo., was the standard for the PCB because the residues in the fishes matched this Aroclor most closely. Standard curves of peak height versus concentration were used to determine the concentrations of components in the extracts. The sensitivity throughout each run was assured by frequent injections of standard solutions. The quantifiable limit was about 0.003 ppm for DDE, TDE, DDT, dieldrin, and endrin, and about 0.04 ppm for PCB depending on daily sensitivity. The mean relative standard deviation for samples analyzed in duplicate was 11%. The average recovery of samples spiked with standards was 85%. The values reported were not corrected for recovery. Residue values were calculated on the basis of micrograms chlorinated hydrocarbon per gram wet tissue or parts per million (ppm).

The PCB were quantitated by summing the peak heights corresponding to the five major peaks in Aroclor 1254 after omitting the twin peak with a retention time similar to that of *p,p'*-DDE. As Veith (1975) also concluded, use of five peaks increased the accuracy of PCB measurement by reducing the effect of minor variations in concentration of individual components in the samples (Figure 1).

Since part of the DDE eluted from silica gel with the PCB fraction and one of the major peaks in Aroclor 1254 overlapped the DDE peak in the gas-chromatographic traces, a special technique was needed to quantitate the DDE in the PCB fraction. First the gross DDE concentration was determined in the usual way from the peak height versus DDE concentration curve. Next, the contribution of PCB to that overlapping peak was calculated based on the assumption that the height of Aroclor peak 3, the peak which overlapped DDE, was proportional to the heights of the five PCB peaks used to calculate the concentration of PCB. To make this calculation, the sum of the peak heights of the five major PCB peaks excluding the "DDE" peak was plotted against the peak height of the "DDE" peak in PCB standards of increasing concentrations. From the sum of the five PCB peaks in the sample, the peak height of the PCB portion of peak 3 in that sample was determined. This peak height was converted to concentration of DDE via the peak height versus concentration curve for DDE. The apparent concentration of DDE from PCB peak 3 was subtracted from the gross DDE concentration in the "DDE" peak to obtain the net concentration of DDE in the PCB fraction. The elctron-capture detector is so much more sensitive to DDE than PCB that this method of calculation affected the accuracy of DDE determination only to a small extent (Figure 1). Use of a minicomputer expedited these calculations.

Confirmation of DDT and its metabolites and PCB was effected by saponifying separate portions of tissue (Reinert 1970). DDT is dehydrochlorinated by base to DDE, and TDE similarly to DDMU. PCB are stable to base. The levels of dieldrin and endrin were too low to warrant confirmation studies.

RESULTS AND DISCUSSION

The marine fishes from the northwestern Atlantic Ocean and northern Gulf of Mexico analyzed in this study contained relatively low levels of ΣDDT and PCB. Of the 70 composite samples, only 29 contained more than 0.05 ppm ΣDDT and 0.1 ppm PCB in the edible portion (skinless fillets), and only one as much as 1 ppm ΣDDT and PCB. Red grouper contained the lowest levels of both chlorinated hydrocarbons. The mean ΣDDT content for

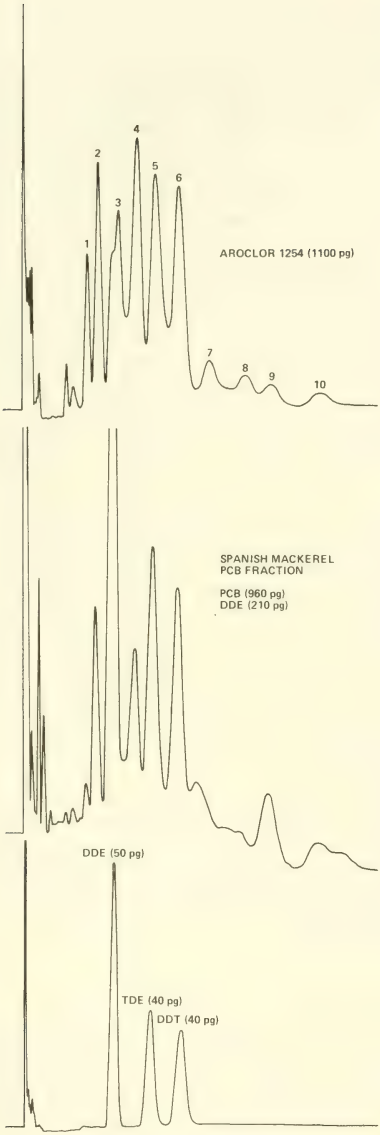


FIGURE 1.—Gas chromatographic curves of Aroclor 1254, the PCB fraction of an extract from Spanish mackerel, and DDT and its metabolites DDE and TDE; pg = picograms or 10^{-12} g.

10 sets of red grouper was 0.008 ppm; for most samples, PCB were not detectable. Black grouper and gag contained slightly higher levels of ΣDDT and PCB. Red snapper also contained little ΣDDT (mean 0.039 ppm), but the PCB level in six samples exceeded 0.1 ppm. Only the two species of mackerel consistently contained quantifiable amounts of both ΣDDT and PCB. The mean levels of ΣDDT were 0.144 ppm in Spanish mackerel and 0.177 ppm in king mackerel. The mean PCB level in both species of mackerel was 0.32 ppm. The highest levels of both chlorinated hydrocarbons were found in one composite sample of king mackerel from the Florida Keys, 0.996 ppm ΣDDT and 1.8 ppm PCB. The data are summarized in Table 2.

The limited data in the literature convey a similar picture. Groupers of the genera *Epinephelus* and *Mycteroperca* from the Gulf of Mexico and the Grand Bahamas contained 0-0.10 ppm ΣDDT and 0.003-0.22 ppm PCB in muscle (Giam et al. 1974). Red snapper from Mobile Bay, Ala., contained 0.086 ppm ΣDDT and 0.14 ppm PCB in the whole animal; gray snapper, *Lutjanus griseus*, from Jacksonville, Fla., 0.007 ppm ΣDDT and no PCB in the whole animal (Markin et al. 1974). Small Spanish mackerel (306 g) from the Savannah River estuary in Georgia contained neither ΣDDT nor PCB in muscle. (Butler[4]) Although somewhat larger than those fish, the smallest fish in the current study (475 g) contained barely detectable amounts of these substances (0.008 ppm ΣDDT and 0.034 ppm PCB). Markin et al. (1974) found 0.04-0.16 ppm ΣDDT and <0.01-0.18 ppm PCB in seven whole Spanish mackerel from the southeastern United States. A single sample of king mackerel muscle from the Gulf of Mexico off Mexico contained 0.024 ppm ΣDDT and 0.034 ppm PCB (Giam et al. 1972). Atlantic mackerel, *Scomber scombrus*, collected in 1971-72 in Canadian waters (Sims et al. 1977) contained more ΣDDT (0.26 ppm) and PCB (0.41 ppm) in the "edible portion" (which may have contained skin and/or bones) than did skinless fillets of either species of mackerel examined in my study. On the other hand, muscle from Atlantic mackerel from the Bay of Fundy-Gulf of Maine contained the same level of PCB (0.35 ppm) (Zitko et al. 1972).

The proportions of *p,p'*-DDT and its metabolites were very similar in the king and Spanish mackerel examined in our study. *p,p'*-DDE is the

[4]Butler, P. A. 1978. EPA-NOAA Cooperative Estuarine Monitoring Program, Final Report, Gulf Breeze, Fla., 108 p.

TABLE 2.—ΣDDT and PCB in fishes from the northwest Atlantic Ocean and Gulf of Mexico. nq = not quantifiable; nd = none detected.

Species	No.[1]	ΣDDT (ppm) Mean±SD	ΣDDT (ppm) Range	PCB (ppm) Mean±SD	PCB (ppm) Range
Gag	8	0.036±0.013	0.017-0.050	0.087±0.023	nq-0.129
Black grouper	5	0.009±0.007	0.003-0.020	nq	nq-0.059
Red grouper	10	0.008±0.007	n.d.-0.025	nd	nd-nq
Red snapper	18	0.039±0.076	n.d.-0.322	0.121±0.108	nd-0.464
King mackerel	18	0.177±0.239	0.009-0.996	0.322±0.414	0.060-1.78
Spanish mackerel	10	0.144±0.097	0.008-0.319	0.319±0.263	0.034-0.821

[1]Number of composites, each consisting of 10 fish.

major component (~65%) accompanied by about 25% of the parent compound and 10% *p,p'*-TDE. Although the composite picture for red snapper looked markedly different (Table 3), in fact the DDT residues in that species actually fell into two categories. In the first group, *p,p'*-TDE and *p,p'*-DDT were not quantifiable, and the maximum content of *p,p'*-DDE was 0.029 ppm. In the second group, five samples containing >0.029 ppm *p,p'*-DDE, both *p,p'*-TDE and *p,p'*-DDT were quantifiable. In those five samples, the proportions of the three components were the same as in the mackerel. Finfish from the Atlantic coast of Canada (Sims et al. 1977) contained proportionately much less *p,p'*-DDE (45%) and more *p,p'*-DDT (40%) and *p,p'*-TDE (15%). The increase in the proportion of *p,p'*-DDE in the present samples may reflect degradation of the parent compound in the environment before it accumulated in the fishes. Samples for the Canadian study were collected in 1971 and 1972, soon after usage of DDT had been drastically curtailed (around 1970) as the result of increasing insect resistance, problems with indirect contamination of foodstuffs, and concern about effects of DDT on nontarget species. Several years elapsed before the samples for the present study were collected, mainly in 1975. In the interval, DDT was degrading aerobically to DDE and anaerobically in the marine environment to TDE. Alternatively, DDT may metabolize more rapidly to DDE in the more temperate climate of the region studied and somewhat less rapidly to TDE.

TABLE 3.—Mean proportions of ΣDDT present as *p,p'*-DDE, *p,p'*-TDE, and *p,p'*-DDT in fishes from the northwest Atlantic Ocean and Gulf of Mexico.

Species	*p,p'*DDE (%) Mean±SD	*p,p'*DDE (%) Range	*p,p'*TDE (%) Mean±SD	*p,p'*TDE (%) Range	*p,p'*-DDT (%) Mean±SD	*p,p'*-DDT (%) Range
Red snapper, all	88±18	58-100	3±5	0-15	9±13	0-30
Red snapper[1]	62± 6	58- 72	10±3	7-15	28± 4	21-32
King mackerel	64± 8	48- 77	8±6	0-17	28± 6	16-40
Spanish mackerel	66±19	48-100	12±8	0-24	21±12	0-37

[1]Five samples which contained >0.029 ppm DDE.

The concentration of PCB, when present, was higher than that of ΣDDT in all samples but one. The mean ratio of PCB to ΣDDT was 1.8 for gag, 2.2 for king and Spanish mackerel, and 2.6 for six sets of red snapper. In the two other samples of red snapper with quantifiable levels of PCB, the PCB/ΣDDT ratios were 22.7 and 24.3. The concentrations of ΣDDT were below 0.01 ppm in both cases. The one sample of red snapper in which the PCB/ΣDDT ratio was below 1 contained a relatively large amount of ΣDDT, 0.096 ppm, the second highest ΣDDT value in the 18 samples of red snapper. In contrast, the PCB concentration was low both in absolute amount, <0.06 ppm, and in rank, 14th out of 18 samples.

The chlorinated-hydrocarbon content of the specimens in this study was, in general terms, directly related to the lipid content. The groupers, which contained <1% lipid, contained the least ΣDDT and PCB. King and Spanish mackerel had the highest lipid contents, 3.5 and 4.6%, respectively, and the highest levels of both ΣDDT and PCB. In three of the six species, the correlation between lipid and ΣDDT was significant, i.e., $P<0.05$. Similarly, in three of the four species for which PCB were quantifiable the correlation between lipid and PCB was significant. Possible relationships between size and chlorinated hydrocarbon content were also examined. Although length, weight, ΣDDT, and PCB were all studied, in no case was a significant correlation found in any of the six species (Table 4). In two of the six species, the correlations between length and lipid and also between weight and lipid were significant. In both species, red snapper and king mackerel, the *P* values for lipid versus chlorinated hydrocarbon, were below 0.01. Giam et al. (1974) noted a relationship between size and concentration of pollutants in groupers from the Gulf of Mexico, but only in the area with the highest contamination, i.e., up to 0.1 ppm.

ΣDDT and PCB levels within single species were compared at the various sites. Fish from the

TABLE 4.—Sample correlation and coefficients (R) and their significance (P) between body dimensions, lipids, and organochlorine residues in fishes from the northwest Atlantic Ocean and Gulf of Mexico.

Species	No.[1]	Length vs. lipid		Weight vs. lipid		Length vs. ΣDDT		Weight vs. ΣDDT		Lipid vs. ΣDDT		Length vs. PCB		Weight vs. PCB		Lipid vs. PCB	
		R	P	R	P	R	P	R	P	R	P	R	P	R	P	R	P
Gag	8	0.369	0.368	0.317	0.444	[2]0.189	0.653	[2]0.232	0.580	[2]0.552	0.156	0.085	0.842	0.117	0.782	0.755	0.030
Black grouper	6	0.102	0.847	0.056	0.917	[2]0.426	0.400	[2]0.356	0.489	[2]0.896	0.016	[3]		[3]		[3]	
Red grouper	10	0.536	0.110	0.595	0.070	[2]0.576	0.082	[2]0.511	0.132	[2] 0.256	0.476	[3]		[3]		[3]	
Red snapper	18	0.571	0.013	0.663	0.003	[2]0.323	0.191	[2]0.438	0.069	[2]0.668	0.002	0.296	0.233	0.374	0.126	0.718	0.001
King mackerel	18	0.575	0.013	0.598	0.009	0.357	0.146	0.333	0.176	0.722	0.001	0.344	0.162	0.333	0.177	0.694	0.001
Spanish mackerel	10	0.035	0.923	0.117	0.747	0.468	0.173	0.417	0.231	0.159	0.661	0.214	0.552	0.209	0.562	0.306	0.390

[1]Number of composites, each consisting of 10 fish.
[2]DDE only, because TDE and DDT not always quantifiable.
[3]PCB not quantifiable.

Florida Keys contained the greatest amounts of both substances, indicating that contamination from agricultural and domestic effluents was greatest in south Florida, an area of intense agriculture and relatively dense population as well. Fish caught in the vicinity of Beaufort and Mobile contained slightly less ΣDDT and PCB. Fish from the other sites contained lower levels of chlorinated hydrocarbons, which were not distinguishable by site, except that only DDE was quantifiable in the one sample from Pascagoula, Miss. The Mississippi River, which receives the runoff from 40% of the land mass of the conterminous United States, including the corn belt and the cotton belt, did not seem to be the main source of either ΣDDT or PCB.

Low levels of dieldrin and endrin, two highly toxic organochlorine pesticides, were found in the fish included in this study. The highest concentration of either compound was 0.026 ppm. The dieldrin and endrin content of only the three species with the highest levels of ΣDDT and PCB were determined. Nonetheless, dieldrin and endrin were quantifiable only in about one-third of the samples. Two of 18 red snapper, 7 of 18 king mackerel, and 6 of 10 Spanish mackerel samples contained quantifiable amounts of both compounds. The mean levels for Spanish mackerel, the species with the highest mean concentrations, were 0.007 ppm dieldrin and 0.008 ppm endrin (Table 5). King mackerel from Aransas Pass contained the highest concentration of dieldrin, 0.026 ppm; Spanish mackerel from Panama City, Fla., the highest concentration of endrin, also 0.026 ppm. The dieldrin and endrin concentrations in the three species followed the same distribution patterns with relation to species and lipid content as was observed for ΣDDT and PCB. Butler (see footnote 4) found no dieldrin in the muscle of small Spanish mackerel from the Savannah River estuary.

CONCLUSIONS

Residues of ΣDDT, PCB, dieldrin, and endrin, although generally low, were found in all species and all locations except Pascagoula, Miss., where only DDE was quantifiable. The highest levels of ΣDDT and PCB, and the only ones to reach 1 ppm, were in one composite sample of king mackerel from the Florida Keys, 0.996 ppm ΣDDT and 1.8 ppm PCB. The highest level of dieldrin, 0.026 ppm, was in king mackerel from Aransas Pass, Tex., and of endrin, also 0.026 ppm, in Spanish mack-

TABLE 5.—Dieldrin and endrin in fishes from the northwest Atlantic Ocean and Gulf of Mexico. nd = not detected; nq = not quantifiable.

Species	No.[1]	Dieldrin (ppm) Mean±SD	Dieldrin (ppm) Range	Endrin (ppm) Mean±SD	Endrin (ppm) Range
Red snapper	18	nd	nd-nq	nd	nd-0.003
King mackerel	18	0.005±0.006	nd-0.026	0.004±0.004	nd-0.014
Spanish mackerel	10	0.007±0.004	nd-0.014	0.008±0.010	nd-0.026

[1]Number of composites, each consisting of 10 fish.

erel from Panama City, Fla. The species with the highest lipid contents contained the highest concentrations of chlorinated hydrocarbons. Significant correlations ($P<0.05$) were found between lipid and size and between lipid and chlorinated hydrocarbon content in two of the six species. In two other species the correlation between lipid and either ΣDDT or PCB was significant. In all cases but one, the chlorinated hydrocarbon levels were substantially below the U.S. Food and Drug Administration guidelines: 5 ppm ΣDDT, 2 ppm PCB, and 0.3 ppm dieldrin and endrin.

ACKNOWLEDGMENTS

I thank the Southeast Fisheries Center Charleston Laboratory, NMFS, NOAA, for providing the samples and Laura G. Lewis for technical support throughout this research. Russell F. Kappenman, Northwest and Alaska Fisheries Center Fisheries Data & Management Systems Division, provided guidance for statistical analyses.

LITERATURE CITED

ANDERSON, D. W., J. R. JEHL, JR., R. W. RISEBROUGH, L. A. WOODS, JR., L. R. DEWEESE, AND W. G. EDGECOMB.
1975. Brown pelicans: Improved reproduction off the southern California coast. Science (Wash., D.C.) 190:806-808.

ANONYMOUS.
1966. Report of a new chemical hazard. New Sci. 32:612.

AULERICH, R. J., R. K. RINGER, AND S. IWAMOTO.
1973. Reproductive failure and mortality in mink fed on Great Lakes fish. J. Reprod. Fertil., Suppl. 19:365-376.

BOWES, G. W., AND C. J. JONKEL.
1975. Presence and distribution of polychlorinated biphenyls (PCB) in arctic and subarctic marine food chains. J. Fish. Res. Board Can. 32:2111-2123.

BURDICK, G. E., E. J. HARRIS, H. J. DEAN, T. M. WALKER, J. SKEA, AND D. COLBY.
1964. The accumulation of DDT in lake trout and the effect on reproduction. Trans. Am. Fish. Soc. 93:127-136.

BURKE, J. A., AND W. HOLSWADE.
1966. A gas chromatographic column for pesticide residue analysis: Retention times and response data. J. Assoc. Off. Anal. Chem. 49:374-388.

BURNETT, R.
1971. DDT residues: Distribution of concentrations in *Emerita analoga* (Stimpson) along coastal California. Science (Wash., D. C.) 174:606-608.

BUTLER, P. A.
1973. Organochlorine residues in estuarine mollusks, 1965-1972—National pesticide monitoring program. Pestic. Monit. J. 6:238-362.

BUTLER, P. A., AND R. L. SCHUTZMANN.
1978. Residues of pesticides and PCBs in estuarine fish, 1972-1976—National pesticide monitoring program. Pestic. Monit. J. 12:51-59.

CARSON, R.
1962. Silent spring. Houghton-Miflin Co., Boston, Mass., 368 p.

GIAM, C. S., A. R. HANKS, R. L. RICHARDSON, W. M. SACKETT, AND M. K. WONG.
1972. DDT, DDE, and polychlorinated biphenyls in biota from the Gulf of Mexico and Caribbean Sea—1971. Pestic. Monit. J. 6:139-143.

GIAM, C. S., R. L. RICHARDSON, D. TAYLOR, AND M. K. WONG.
1974. DDT, DDE and PCBs in the tissues of reef dwelling groupers (Serranidae) in the Gulf of Mexico and the Grand Bahamas. Bull. Environ. Contam. Toxicol. 11:189-192.

GOLDBERG, E. D., V. T. BOWEN, J. W. FARRINGTON, G. HARVEY, J. H. MARTIN, P. L. PARKER, R. W. RISEBROUGH, W. ROBERTSON, E. SCHNEIDER, AND E. GAMBLE.
1978. The mussel watch. Environ. Conserv. 5:101-125.

HENDERSON, C., A. INGLIS, AND W. L. JOHNSON.
1971. Organochlorine insecticide residues in fish—Fall 1969 National pesticide monitoring program. Pestic. Monit. J. 5:1-11.

HENDERSON, C., W. L. JOHNSON, AND A. INGLIS.
1969. Organochlorine insecticide residues in fish (National pesticide monitoring program). Pestic. Monit. J. 3:145-171.

JENSEN, S., A. G. JOHNELS, M. OLSSON, AND G. OTTERLIND.
1969. DDT and PCB in marine animals from Swedish waters. Nature (Lond.) 224:247-250.

LEBOEUF, B. J., AND M. L. BONNELL.
1971. DDT in California sea lions. Nature (Lond.) 234:108-110.

LIEB, A. J., D. D. BILLS, AND R. O. SINNHUBER.
1974. Accumulation of dietary polychlorinated biphenyls (Aroclor 1254) by rainbow trout (*Salmo gairdneri*). J. Agric. Food Chem. 22:638-642.

MARKIN, G. P., J. C. HAWTHORNE, H. L. COLLINS, AND J. H. FORD.
1974. Levels of mirex and some other organochlorine residues in seafood from Atlantic and Gulf coastal states. Pestic. Monit. J. 7:139-143.

MCDERMOTT-EHRLICH, D., D. R. YOUNG, AND T. C. HEESEN.
1978. DDT and PCB in flatfish around southern California municipal outfalls. Chemosphere 6, p. 453-461.

MEARNS, A. J., AND M. J. SHERWOOD.
1977. Distribution of neoplasms and other diseases in marine fishes relative to the discharge of waste water. Ann. N.Y. Acad. Sci. 298:210-224.

REINERT, R. E.
1970. Pesticide concentrations in Great Lakes fish. Pestic. Monit. J. 3:233-240.

RISEBROUGH, R. W., W. WALKER II, T. T. SCHMIDT, B. W. DE LAPPE, AND C. W. CONNORS.
1976. Transfer of chlorinated biphenyls to Antarctica. Nature (Lond.) 264:738-739.

SIMS, G. G., J. R. CAMPBELL, F. ZEMLYAK, AND J. M. GRAHAM.
1977. Organochlorine residues in fish and fishery products from the Northwest Atlantic. Bull. Environ. Contam. Toxicol. 18:697-705.

SLADEN, W. J. L., C. M. MENZIE, AND W. L. REICHEL.
1966. DDT residues in Adelie penguins and a crabeater seal from Antarctica. Nature (Lond.) 210:670-673.

SNYDER, D., AND R. REINERT.
1971. Rapid separation of polychlorinated biphenyls from DDT and its analogues on silica gel. Bull. Environ. Contam. Toxicol. 6:385-390.

STOUT, V. F., AND F. L. BEEZHOLD.
1979. Analysis of chlorinated hydrocarbon pollutants: A simplified extraction and cleanup procedure for fishery products. Fish. Bull., U.S. 76:880-886.

VEITH, G. D.
1975. Baseline concentrations of polychlorinated biphenyls and DDT in Lake Michigan fish, 1971. Pestic. Monit. J. 9:21-29.

YOUNG, D. R., D. J. MCDERMOTT, AND T. C. HEESEN.
1976. DDT in sediments and organisms around southern California outfalls. J. Water Pollut. Control Fed. 48:1919-1928.

ZITKO, V.
1978. The interference of aromatic hydrocarbons in the determination of PCB's. Proceedings, 4th Joint Conference on Sensing of Environmental Pollutants, American Chemical Society, Pap. 201, p. 757-760.

ZITKO, V., O. HUTZINGER, AND P. M. K. CHOI.
1972. Contamination of the Bay of Fundy—Gulf of Maine area with polychlorinated biphenyls, polychlorinated terphenyls, chlorinated dibenzodioxins, and dibenzofurans. Environ. Health Perspect. 1:47-50.

SYSTEMATICS AND DISTRIBUTION OF CERATIOID ANGLERFISHES OF THE FAMILY MELANOCETIDAE WITH THE DESCRIPTION OF A NEW SPECIES FROM THE EASTERN NORTH PACIFIC OCEAN[1]

THEODORE W. PIETSCH AND JOHN P. VAN DUZER[2]

ABSTRACT

The ceratioid anglerfish family Melanocetidae is revised on the basis of a study of approximately 600 specimens collected from all oceans. Of the 11 nominal species of *Melanocetus* based on females, 4 are recognized: *M. johnsoni*, with *M. krechi, M. rotundatus, M. ferox, M. cirrifer*, and *M. megalodontis* as synonyms; *M. polyactis*; *M. niger*; and *M. murrayi*, with *M. vorax* and *M. tumidus* as synonyms. A fifth species is newly described from a single female collected from the eastern Pacific Ocean off Mazatlan, Sinaloa, Mexico. The new form differs most strikingly from its allies in having a larger escal bulb and shorter jaw teeth.

Melanocetus is widely distributed throughout all the major oceans of the world between about 250 m and some unknown lower depth limit that exceeds 3,000 m. *Melanocetus johnsoni* and *M. murrayi* are wide ranging forms, whereas *M. polyactis* and *M. niger* are apparently restricted to the eastern tropical Pacific.

Melanocetus murrayi appears to be the most phylogenetically derived member of the family. The four remaining species are much more closely related to each other than any is to *M. murrayi*. *Melanocetus johnsoni* is perhaps derived in having a relatively long illicium, and in having fewer, but longer jaw teeth. *Melanocetus polyactis* and *M. niger* are similar in having relatively short jaw teeth, a similar escal morphology, and a sympatric geographic distribution that is limited to the eastern tropical Pacific. The newly described form is derived in having an extremely large escal bulb, comparable with no other known ceratioid.

The Melanocetidae include globose, bathypelagic anglerfishes, easily separated from members of allied families by having 12 or more dorsal fin rays, 3 or 4 anal rays, and large, fanglike jaw teeth (Bertelsen 1951; Pietsch 1972a). The only recognized genus of the family was established by Günther (1864) with the description of *Melanocetus johnsoni*, based on a single female specimen collected in the Atlantic Ocean, off Madeira. Since that time, 10 additional species based on females have been described (Table 1). From a comparison of the characters used to distinguish these nominal forms, Bertelsen (1951, table 4) doubted that *M. krechi* and *M. cirrifer* could be maintained and that *M. ferox* and *M. niger* might be synonyms. *Melanocetus murrayi* and *M. johnsoni* were recognized as the only species known from the Atlantic; *M. niger, M. ferox,* and *M. polyactis* were considered forms restricted to the eastern tropical Pacific. Six larval specimens from the Gulf of Panama were assigned to *M. polyactis*. The remaining larvae (approximately 600 individuals) were separated into two groups, representing *M. murrayi* and *M. johnsoni*, on the basis of geographic distribution, fin ray counts, and a comparison of larval and adolescent female pigmentation. Despite these allocations, Bertelsen (1951) made it clear that ". . . the separation of the species is still very uncertain and future investigations and material will probably make it necessary to revise this synopsis."

At the time of Bertelsen's (1951) monograph on the Ceratioidei, 19 metamorphosed melanocetid males were known. Of these, 14 had been set up as types of 12 separate species, and 5 were uncertainly placed. On the basis of subdermal pigment, fin ray counts, and geographic distribution, Bertelsen (1951) synonymized 6 of these 12 nominal forms with *M. johnsoni* and 4 with *M. murrayi*. The remaining two species based on males, *M. longirostris* and *M. nudus*, each differing slightly from the rest of the material, were tentatively retained (Table 1).

With the vast increase in the amount of material of *Melanocetus* made available in the last 25

[1]Contribution No. 516 from the College of Fisheries, University of Washington, Seattle, WA 98195.

[2]College of Fisheries, University of Washington, Seattle, WA 98195.

Manuscript accepted September 1979.
FISHERY BULLETIN: VOL. 78, NO. 1, 1980.

TABLE 1.—Reallocation of nominal forms of *Melanocetus*. Valid names on right. Synonymy for species based on males after Bertelsen 1951.

Females:	
Melanocetus johnsoni Günther 1864	*Melanocetus johnsoni* Günther 1864
Melanocetus krechi Brauer 1902	
Melanocetus rotundatus Gilchrist 1903	
Melanocetus ferox Regan 1926	
Melanocetus cirrifer Regan and Trewavas 1932	
Melanocetus megalodontis Beebe and Crane 1947	
Melanocetus polyactis Regan 1925	*Melanocetus polyactis* Regan 1925
Melanocetus niger Regan 1925 (in part)	
Melanocetus niger Regan 1925 (in part)	*Melanocetus niger* 1925
Melanocetus murrayi Günther 1887	*Melanocetus murrayi* Günther 1887
Melanocetus vorax Brauer 1902	
Melanocetus tumidus Parr 1927	
Males:	
Centrocetus spinulosus Regan and Trewavas 1932	*Melanocetus johnsoni* Günther 1864
Xenoceratias micracanthus Regan and Trewavas 1932	
Xenoceratias heterorhynchus Regan and Trewavas 1932	
Xenoceratias laevis Regan and Trewavas 1932	
Xenoceratias brevirostris Regan and Trewavas 1932	
Xenoceratias braueri Koefoed 1944	
Rhynchoceratias rostratus Regan 1926 (in part)	*Melanocetus polyactis* Regan 1925
Rhynchoceratias leucorhinus Regan 1926 (in part)	
Rhynchoceratias acanthirostris Parr 1927	*Melanocetus murrayi* Günther 1887
Rhynchoceratias latirhinus Parr 1927	
Rhynchoceratias longipinnis Parr 1930	
Xenoceratias regani Koefoed 1944	

yr, we are able to recognize five species based on females. Four of these are previously described forms: *M. johnsoni,* represented by 346 specimens collected from all three major oceans of the world; *M. polyactis* and *M. niger*, known from 15 and 6 specimens both restricted to the eastern tropical Pacific; and *M. murrayi*, 140 specimens of worldwide distribution. The fifth is a new species recently collected by the *Velero IV* of the University of Southern California in the eastern Pacific off Mazatlán, Sinaloa, Mexico. It differs strikingly from its allies in having a considerably larger escal bulb and shorter jaw teeth.

Although the number of known male specimens has increased nearly fourfold since Bertelsen's (1951) work, no new diagnostic data are available. We have examined 73 individuals (11.5-24 mm standard length), none of which can be satisfactorily identified to species based on females. As predicted by Bertelsen (1951), the variation in the number of denticular teeth is greater than previously thought and values given in his key overlap to a much greater extent than is indicated. An attempt to utilize differences in larval pigmentation, thought to be more or less retained, at least in the younger metamorphosed males, failed to separate the material into groups that could be associated with species based on females. Although Bertelsen's (1951) synonymies for nominal species based on males are retained here, additional male specimens are listed as *Melanocetus* sp.

METHODS AND MATERIALS

Standard lengths (SL) are used throughout unless otherwise stated. Measurements were taken from the left side whenever possible and rounded to the nearest 0.5 mm. To ensure accurate fin ray counts, skin was removed from the pectoral fins and incisions were made to reveal the rays of the dorsal and anal fins. Sockets, indicating missing teeth in the jaws and on the vomer, were included in total tooth counts. Jaw tooth counts are the sum of both right and left sides. Head depth is the distance from the tip of the sphenotic spine to the base of the quadrate spine. Head width is the distance between the anterolateralmost margins of the sphenotic bones. Lower jaw length is the distance from the symphysial spine to the posteriormost margin of the articular. Illicium length is the distance from the articulation of the pterygiophore of the illicium and the illicial bone to the distal surface of the esca, excluding escal appendages. The width of the pectoral fin lobe is the distance between the point of articulation of the uppermost fin ray to the articulation of the lowermost fin ray. Terminology used in describing the various parts of the angling apparatus follows Bradbury (1967). Definitions of terms used for the different stages of development follow Bertelsen (1951). Complete locality data are given for primary type material only.

The comparative osteological investigation was

based primarily on five female specimens (two *M. murrayi*, 75 and 84 mm SL, and three *M. johnsoni*, 44.5, 60, and 75 mm SL; material representing the remaining species of the genus was unavailable) cleared and stained with Alizarin red S following the trypsin digestion technique (Taylor 1967). Bone terminology follows Pietsch (1974).

Unless otherwise indicated, all diagnoses and descriptions are based on female specimens >20 mm SL. For males and larvae see Bertelsen (1951). Material is catalogued in the following institutions: Australian Museum, Sydney (AMS); British Museum (Natural History), London (BMNH); Bingham Oceanographic Collections, Peabody Museum of Natural History, Yale University (BOC); California Academy of Sciences, San Francisco (CAS); Florida State Museum, University of Florida, Gainsville (FSM); Institute of Oceanology, Academy of Sciences, U.S.S.R., Moscow (IOAN); Institute of Oceanographic Sciences, Surrey, England (IOS); Institut für Seefischerei, Hamburg (ISH); Natural History Museum of Los Angeles County (LACM); Museum of Comparative Zoology, Harvard University (MCZ); National Museum of New Zealand, Wellington (NMNZ); Royal Ontario Museum, Toronto (ROM); South African Museum, Cape Town (SAM); University of Bergen, Zoological Museum (UBZM); University of Miami Marine laboratory, (UMML); National Museum of Natural History, Washington, D.C. (USNM); Virginia Institute of Marine Science, Gloucester Point (VIMS); Zoological Museum, Humboldt University, Berlin (ZMHU); Zoological Museum, University of Copenhagen (ZMUC).

OSTEOLOGY OF FEMALES

The osteology of *Melanocetus* was partially described by Regan (1926, fig. 10), Parr (1930a, fig. 2-5, male only), Regan and Trewavas (1932, fig. 19-28), and Bertelsen (1951, fig. 13, 14). In the following account, only those comparative aspects that need amending or that have not previously appeared in the literature are discussed.

Cranium (Figures 1-9). — The anterior portion of the cranium of *Melanocetus* is considerably wider, relative to the posterior portion, than in other ceratioids; the distance between the lateral margins of the ethmoid cartilage is nearly equal to the

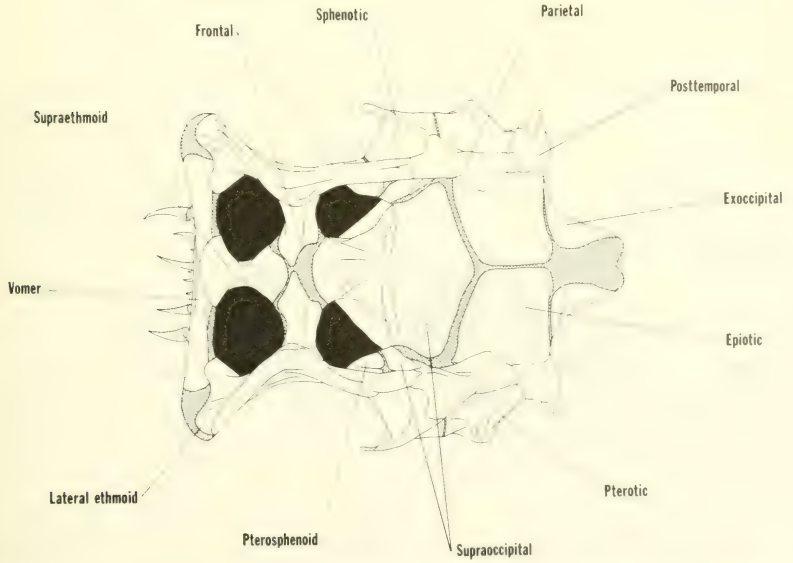


FIGURE 1.—Dorsal view of cranium of *Melanocetus johnsoni*, LACM 32786-1, 75 mm SL. Cartilage stippled, open spaces solid black.

distance between the tips of the sphenotic bones (Figures 1, 2) The head of the vomer, bearing as many as 10 recurved teeth, is also unusually wide (Figures 1, 2, 5-7). The frontals are triradiate in shape and widely separated from each other along their dorsal margins, approaching one another on the midline only at their ventromedial extensions. A semicircular-shaped pterosphenoid is present under the posterior extension of each frontal. The parasphenoid is well separated from the ventromedial extensions of the frontals. Posteromedially, the parasphenoid underlies the anterior

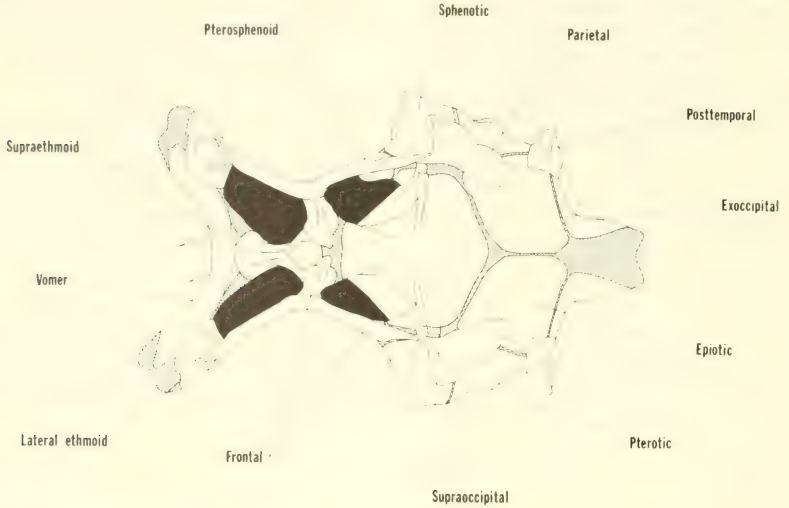


FIGURE 2.—Dorsal view of cranium of *Melanocetus murrayi*, LACM 31501-3, 84 mm SL. Cartilage stippled, open spaces solid black.

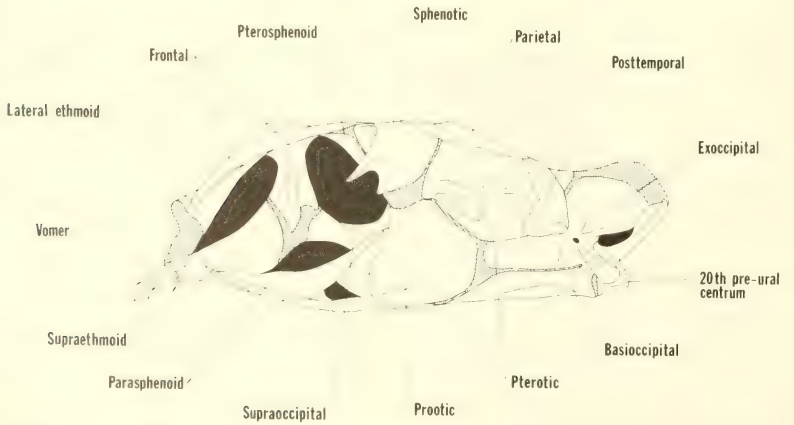


FIGURE 3.—Lateral view of cranium of *Melanocetus johnsoni*, LACM 32786-1, 75 mm SL. Cartilage stippled, open spaces solid black.

projection of the supraoccipital; posteriorly directed dorsolateral extensions of the parasphenoid make contact laterally with the respective prootic (Figures 3, 4).

The large prootics are separated from each other anteriorly by the anterior process of the supraoccipital. Ventrally, each prootic forms a relatively large, anterolaterally directed, conical projection not found in other ceratioids (Figures 3-5, 8).

The supraoccipital is the largest element of the cranium, making up a considerable portion of the roof of the cranium. Together with the frontals, the supraoccipital forms the floor of a deep, V-shaped illicial trough (Figure 8). An anteriorly directed extension of the supraoccipital that sep-

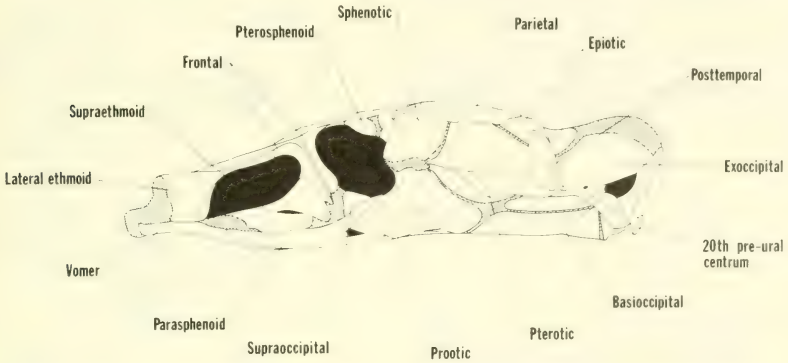


FIGURE 4.—Lateral view of cranium of *Melanocetus murrayi*, LACM 31501-3, 84 mm SL. Cartilage stippled, open spaces solid black.

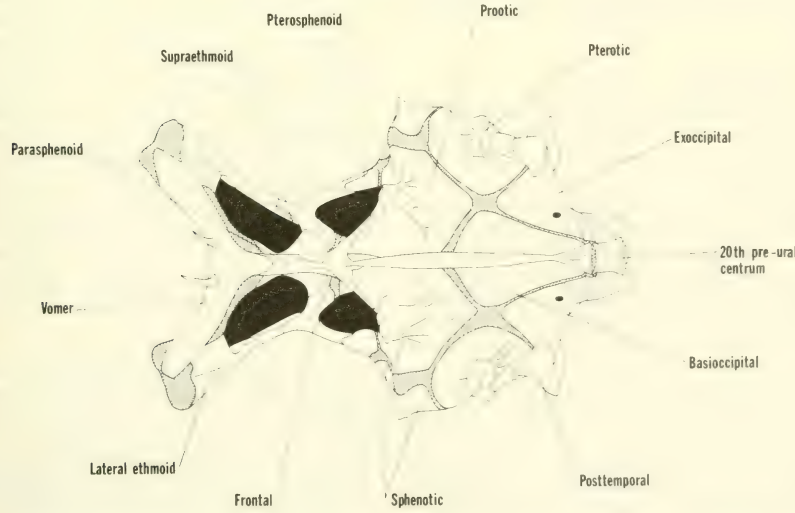


FIGURE 5.—Ventral view of cranium of *Melanocetus murrayi*, LACM 31501-3, 84 mm SL. Cartilage stippled, open spaces solid black.

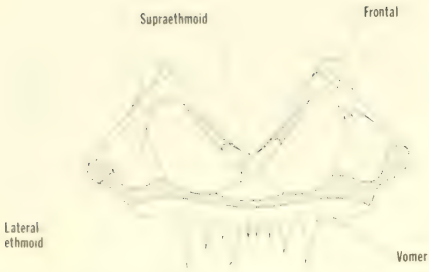


FIGURE 6.—Anterior view of anterior half of cranium of *Melanocetus johnsoni*, LACM 32786-1, 75 mm SL. Cartilage stippled.

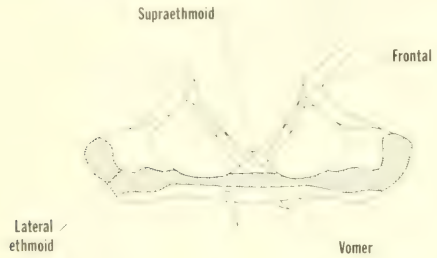


FIGURE 7.—Anterior view of anterior half of cranium of *Melanocetus murrayi*, LACM 31501-3, 84 mm SL. Cartilage stippled.

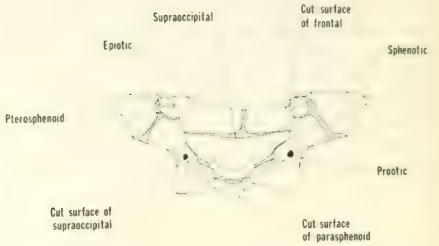


FIGURE 8.—Anterior view of posterior half of cranium of *Melanocetus murrayi*, LACM 31501-3, 84 mm SL, anterior portion removed. Cartilage stippled.

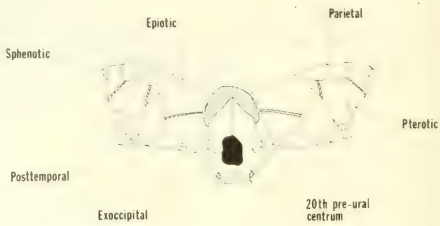


FIGURE 9.—Posterior view of cranium of *Melanocetus murrayi*, LACM 31501-3, 84 mm SL. Cartilage stippled.

arates the prootics on the midline, is narrowly separated by cartilage from the ends of the ventromedial extensions of the frontals. The supraoccipital is not overlapped by the parietals (Figures 1-5).

The cranium of *M. murrayi* is considerably more elongate and compressed compared with that of its congeners (Figures 3, 4). As a consequence, the anterior margin of the vomer of *M. murrayi* is deeply concave (nearly straight in other forms), the frontals are more elongate and considerably lighter in construction, the sphenotics are much less produced forward, and the parietals do not extend posteriorly to overlap the posttemporals as they do in other *Melanocetus* species (Figures 1, 2).

Mandibular arch (Figures 10, 11).—The anterior portion of the premaxilla bears a short ascending process and a slightly longer articular process. A small (compared with those of oneirodids, Pietsch 1974) symphysial cartilage lies just behind the posteriorly notched symphysis of the premaxillae. There is no postmaxillary process of the premaxilla. The elongate portion of each premaxilla may bear up to 89 recurved, depressible teeth of mixed sizes (Figure 10).

On each side, the posterior ends of the premaxilla and maxilla are united by connective tissue to each other and to the lateral surface of the ascending process of the articular of the lower jaw, preventing any forward rotation of the upper jaw bones to close off the corners of the mouth. There is no elongate, anterior maxillomandibular ligament originating on the dentary as in oneirodids (labial cartilage of Le Danois 1964; Pietsch 1972a, 1974).

The dentaries meet on the midline to form a strong symphysial spine. Each dentary may bear up to 71 recurved, depressible teeth of mixed sizes (Figure 11).

Palatine and hyoid arches (Figures 11, 12). — The distal portion of the palatine arch (including the mesopterygoid, ectopterygoid, and palatine) is elongate and slender throughout (Figure 11). The small mesopterygoid is in contact with the metap-

terygoid. The suspensorium is unusually narrow and elongate (due largely to the extremely narrow and elongate quadrate), and directed obliquely backward. The posterior head of the hyomandibular is the larger of the two heads forming a broad articulation with the pterotic. The interhyal is short and relatively thick (compared with that of oneirodids, Pietsch 1974).

The hyoid apparatus (including epihyal, ceratohyal, and upper and lower hypohyals) is relatively short and thick (Figure 12). The lower hypohyal extends down beyond the ventral margin of the ceratohyal. In other ways this portion of the hyoid arch does not differ substantially from that described for oneirodids (Pietsch 1974).

Opercular apparatus (Figure 11). — The opercular apparatus is somewhat reduced (compared with that of oneirodids, Pietsch 1974). The opercle

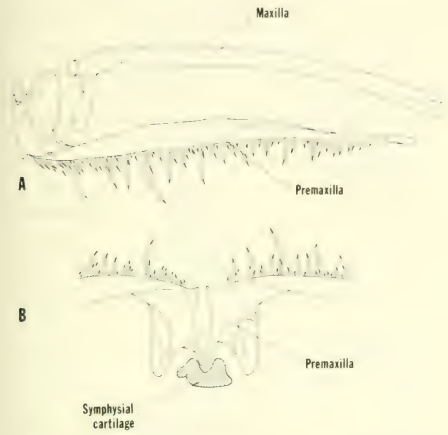


FIGURE 10.—Elements of upper jaw of *Melanocetus murrayi*, LACM 31501-3, 84 mm SL: A. Maxilla and premaxilla, left lateral view; B. Symphysis of premaxillae, dorsal view.

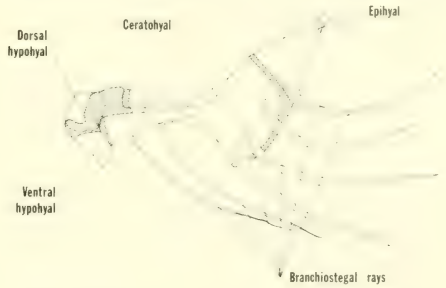


FIGURE 12.—Lateral view of hyoid apparatus of *Melanocetus murrayi*, LACM 31501-3, 84 mm SL, interhyal not shown. Cartilage stippled.

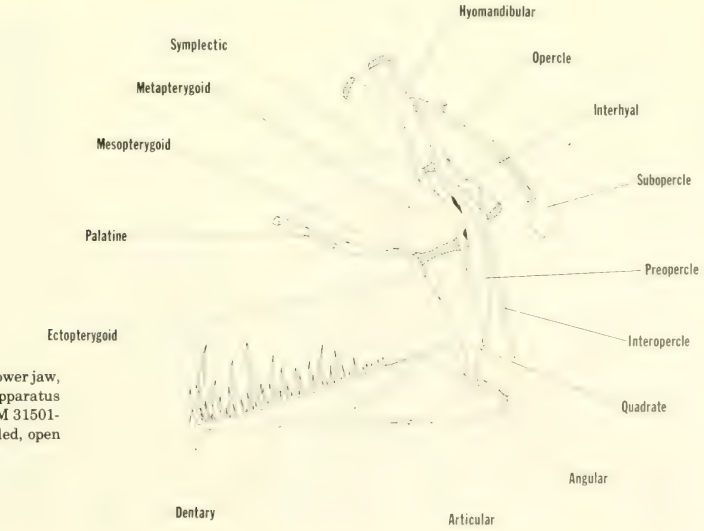


FIGURE 11.—Lateral view of lower jaw, suspensorium, and opercular apparatus of *Melanocetus murrayi*, LACM 31501-3, 84 mm SL. Cartilage stippled, open spaces solid black.

is notched posteriorly, but the upper fork of this bone is considerably shorter than the lower fork and sometimes absent. The subopercle is narrow and elongate, the upper part tapering to a fine point, the lower part rounded with a well-developed anterior spine or projection. The interopercle is unusually long and slender. The preopercle is more or less straight.

Branchial arches (Figure 13). — Pharyngobranchials I and IV are absent; those of the second and third arches are well developed, bearing four to nine recurved and depressible fangs. Epibranchial I is reduced lying free in the connective tissue matrix. Ceratobranchial V is also reduced but tightly connected to the medial-proximal margin of ceratobranchial IV. There are three hypobranchials, and a single basibranchial ossification surrounded by a triangular-shaped cartilage.

Vertebrae and caudal skeleton (Figure 14).—The vertebral column forms a sigmoid curve, dipping down behind the region of the gut and sloping up again to support the tail. In the five cleared and stained specimens examined there are 20 vertebral centra (including the half-centrum to which is

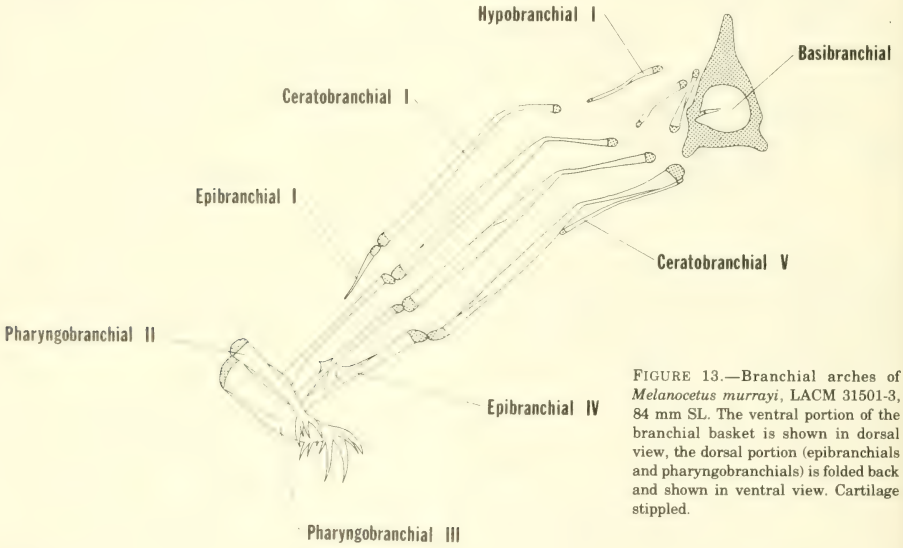


FIGURE 13.—Branchial arches of *Melanocetus murrayi*, LACM 31501-3, 84 mm SL. The ventral portion of the branchial basket is shown in dorsal view, the dorsal portion (epibranchials and pharyngobranchials) is folded back and shown in ventral view. Cartilage stippled.

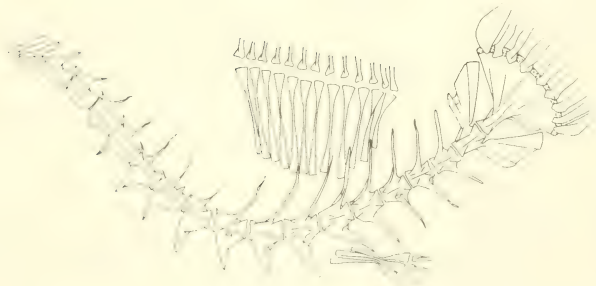


FIGURE 14.—Lateral view of vertebral column, dorsal and anal fins, and caudal skeleton of *Melanocetus murrayi*, LACM 31501-3, 84 mm SL. Cartilage stippled.

fused the hypural plate, Pietsch 1972a) of which 13-15 are caudal vertebrae (those bearing complete haemal arches). Epurals are absent. The hypural plate is unnotched posteriorly and bears the overlapping bases of nine principal caudal rays, the uppermost of which is exceptionally large. The uppermost and two lowermost caudal rays are simple, the central rays are bifurcated distally.

Median fins and illicial apparatus (Figures 14, 15). — There are 13-19 biserial, segmented, and unbranched dorsal fin rays, the number varying somewhat among species. The rays are supported by elongate, closely associated radials, usually one less than the number of rays. All species of the genus have 4 anal fin rays (of 353 specimens counted, only 2 had 3 anal rays, and only 2 had 5 rays) that are like those of the dorsal fin, invariably supported by 3 similar, closely associated radials (Table 2, Figure 14).

The pterygiophore of the illicium is strongly compressed with a thin, bladelike ventral expansion. The length of the pterygiophore varies from 17% SL in *M. murrayi* to 33% SL in *M. johnsoni*. The remnant of the second cephalic ray is a minute ossification lying on the pterygiophore just behind the articulation with the illicial bone (Figure 15). The length of the illicial bone varies slightly among *Melanocetus* species, becoming longer proportionately with growth.

Pectoral girdle, pectoral fin, and pelvic bone (Figure 16).—Each posttemporal overlaps the respective pterotic, epiotic, and exoccipital. It is in turn overlapped by the parietal in *M. johnsoni*, but widely separated from this bone in *M. murrayi*.

An ossified posteroventral process of the coracoid is absent but perhaps represented by a posteroventral cartilaginous extension. There are four pectoral radials, the lower two of which become completely fused with each other giving the appearance of only three radials (Regan and Trewavas 1932, fig. 22; Pietsch 1972a).

The pectoral fin lobe of *M. murrayi* is considerably smaller than that of other *Melanocetus* species (Figure 16A). In other ways the elements of the pectoral girdle, pectoral fin, and pelvic bone do not differ substantially from those of oneirodids (Pietsch 1974).

Skin spines.—Minute dermal spines (approximately 0.03-0.11 mm long) are present in the skin

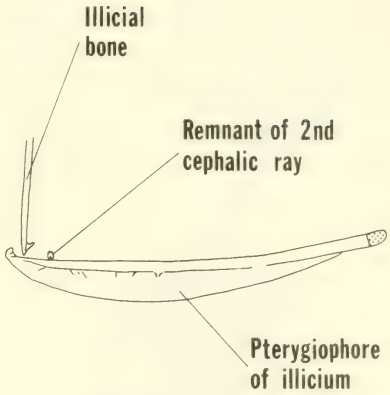


FIGURE 15.—Bones of illicial apparatus of *Melanocetus murrayi*, LACM 31501-3, 84 mm SL, left lateral view. Cartilage stippled.

of the two species examined osteologically. In *M. johnsoni* they are most numerous on the side of the trunk under the dorsal fin (where there are about 6 spines/mm^2) but become progressively more widely scattered anteriorly and finally disappear in the area of the upper and lower jaws (Struhsaker 1962). In the two specimens of *M. murrayi* examined osteologically the spines are confined to the caudal peduncle.

SYSTEMATICS

Family Melanocetidae Regan 1912

Type genus *Melanocetus* Günther 1864

Diagnosis. — The metamorphosed females of the Melanocetidae are distinguished from those of all other ceratioid families by having the following combination of characters: jaws equal anteriorly; supraethmoid present; parietals present; pterosphenoid present; anterior maxillomandibular ligament absent (Pietsch 1972a); hyomandibular with a double head; hypohyals 2; branchiostegal rays 6; operculum bifurcate, upper fork reduced; suboperculum slender, as long as lower fork of operculum, with strong anterior spine; pharyngobranchials I and IV absent; epibranchial I reduced; a single ossified basibranchial; epibranchial and ceratobranchial teeth absent; epurals absent; only an ossified remnant of second cephalic ray present; dorsal fin rays 13-17, anal fin

TABLE 2.—Fin ray frequencies for females of *Melanocetus* species.

Species	Dorsal						Anal			Pectoral (both sides)								
	12	13	14	15	16	17	3	4	5	15	16	17	18	19	20	21	22	23
Melanocetus johnsoni		6	70	64	2	1	1	136	1			13	34	69	36	12	2	1
Melanocetus polyactis			4	4	4	2		13	1			2	3	12	4	2	1	
Melanocetus niger			3	2				5					2	2	5	1		
Melanocetus eustalus				1				1			2							
Melanocetus murrayi	1	32	29					62		5	17	37	8	5	1			
Total	1	38	106	71	6	3	1	217	2	5	19	52	47	88	46	15	3	1

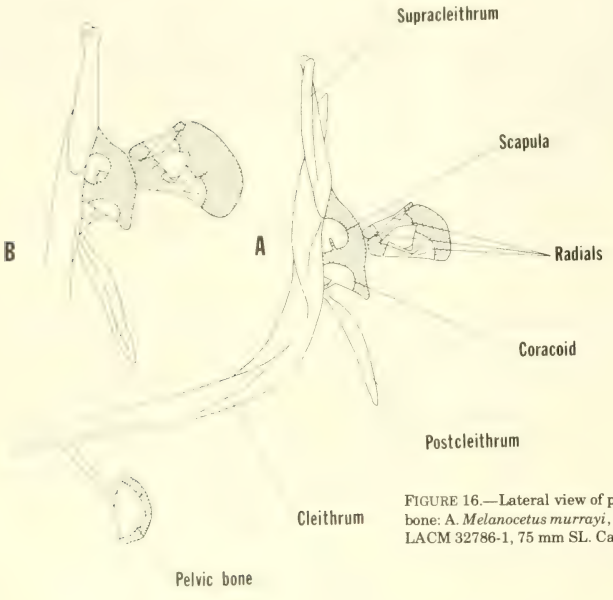


FIGURE 16.—Lateral view of pectoral girdle, pectoral radials, and pelvic bone: A. *Melanocetus murrayi*, LACM 31501-3, 84 mm SL; B. *M. johnsoni*, LACM 32786-1, 75 mm SL. Cartilage stippled.

rays 4 (rarely 3 or 5), caudal fin rays 9 (1-6-2); ossified posteroventral process of coracoid absent; pectoral radials 4, fusing to 3 with growth; pelvic bones expanded distally; esca without denticles; minute, widely spaced skin spines present in at least some species.

The metamorphosed males of the Melanocetidae are distinguished from those of all other ceratioid families in having the following combination of characters: free-living; jaw teeth absent; upper denticular with 2-3 semicircular series of strong, recurved denticles, fused with a median series of 3-9 enlarged dermal spines that articulate with the pterygiophore of the illicium; lower denticular with 10-23 recurved denticles, fused into a median and two lateral groups; eyes directed laterally, elliptical in shape, pupil larger than lens; olfactory organs large, nostrils lateral, nasal area unpigmented, inflated; dorsal fin rays 12-16, anal fin rays 4, caudal fin rays 9 (1-6-2); skin spinulose or naked.

Description. — Females relatively short and deep, globular (but often appearing highly compressed apparently due to deformation upon capture, compare Figures 17, 18); head short; mouth large, nearly vertical, cleft not extending past eye; lower jaw with a well-developed symphysial spine; oral valve weakly developed; two nostrils on each side on distal surface of a rounded papilla; eye small, subcutaneous, appearing through a circular, translucent area of integument within a shallow, orbital pit formed between sphenotic and frontal bones; gill opening oval in shape, situated posteri-

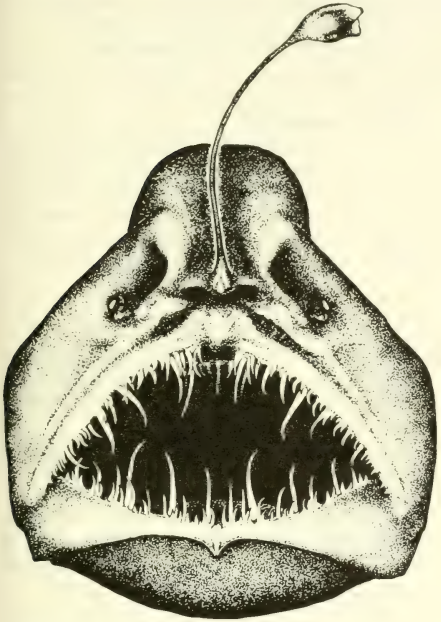


FIGURE 17.—Anterior view of *Melanocetus johnsoni*, LACM 31484-1, 85 mm SL. Drawn by Elizabeth Anne Hoxie.

or to pectoral lobe; all four epibranchials closely bound together by connective tissue; anterior half of ceratobranchial I bound to medial surface of ceratohyal by connective tissue, posterior half free; gill filaments present on anteriormost tip of ceratobranchial I and full length of ceratobranchials II through IV; pseudobranch absent; no opening behind fourth gill arch; ovaries paired; pyloric caeca absent.

Illicial length 23.1-60.8% SL; anteriormost tip of pterygiophore of illicium exposed, emerging on snout between eyes, its posterior end concealed under skin; escal bulb simple, usually with a rounded or conical, distal prolongation, and often with posterior and anterior crests; elongate appendages and filaments absent.

Jaw teeth slender, recurved, and depressible, some slightly hooked distally, those in lower jaw less numerous, but slightly longer than those in upper jaw; number of teeth in lower jaw 32-142, in upper jaw 29-178; longest tooth in lower jaw 6.9-

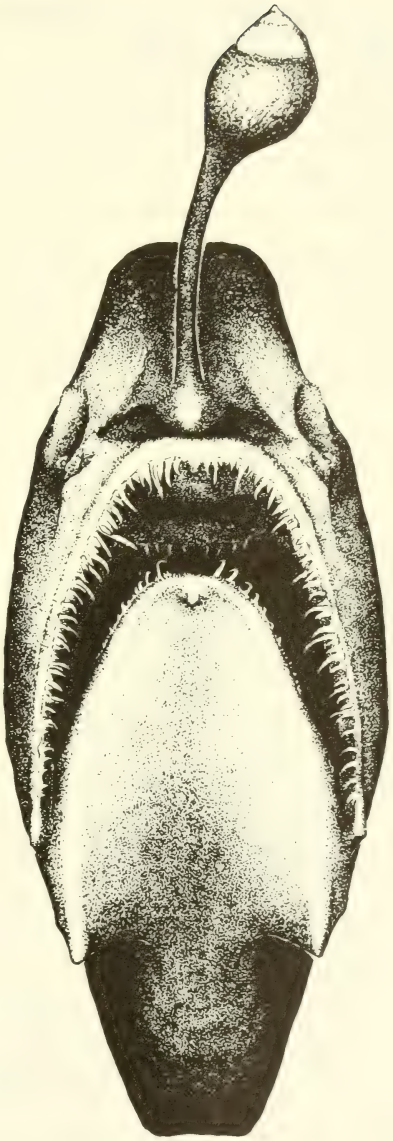


FIGURE 18.—Holotype of *Melanocetus eustalus*, LACM 30037-12, 111 mm SL, anterior view. Drawn by Elizabeth Anne Hoxie.

25.0% SL; vomer with 0-12 teeth; pharyngobranchials II and III heavily toothed.

Color in preservative dark brown to black over entire surface of body (except for distal portion of escal bulb) and oral cavity; all fins colorless in specimens less than about 40 mm SL (except for caudal rays in adolescent *M. murrayi*, Bertelsen 1951, fig. 16I).

Pectoral fin rays 15-23 (Table 2); pelvic fins absent.

The following measurements, in percent of standard length, are summarized for females (20-120 mm SL) of all species: head depth 42.5-82.0; least outside width between frontals 9.1-28.6; head width 22.6-45.0; premaxillary length 36.3-76.0; lower jaw length 36.7-78.0; width of pectoral fin lobe 6.1-17.8; escal bulb width 1.9-11.3

For description of males see Diagnosis above and Bertelsen (1951).

Genus *Melanocetus* Günther 1864

Females

Melanocetus Günther 1864:301-302, pl. 25 (type species *Melanocetus johnsoni* Günther 1864, by monotypy).

Melanocetus (subgenus *Liocetus*) Günther 1887:56, pl. 11, fig. A (type species *Melanocetus murrayi* Günther 1887, by monotypy).

Liocetus Goode and Bean 1896: 495-496, fig. 407 (type species *Melanocetus murrayi* Günther 1887, by monotypy).

Melanocoetus Smith 1949:429 (erroneous spelling of *Melanocetus*, therefore taking the same type species, *Melanocetus johnsoni* Günther 1864).

Linocetus Bertelsen 1951:40, 44 (erroneous spelling of *Liocetus*, therefore taking the same type species, *Melanocetus murrayi* Günther 1887).

Males

Rhynchoceratias Parr 1927:30-33, fig. 11-12 (in part; type species *Rhynchoceratias brevirostris* Regan 1925, by subsequent designation of Fowler 1936).

Centrocetus Regan and Trewavas 1932:53, fig. 79 (type species *Centrocetus spinulosus* Regan and Trewavas 1932, by monotypy).

Xenoceratias Regan and Trewavas 1932:54-57, fig. 80-84 (type species *Xenoceratias longirostris* Regan and Trewavas 1932, by subsequent designation of Fowler 1936).

Diagnosis and description same as for family.

Key to Species Based on Females

The following key will differentiate female specimens >20 mm SL (for males and larvae see Bertelsen 1951). The key should be used in conjunction with Figures 19-24.

1A. Escal bulb width 11.3% SL in 111 mm specimen (Figures 18, 28); longest lower jaw tooth 5.9% SL in 111 mm specimen ..... *Melanocetus eustalus* n. sp. (single known female)

1B. Escal bulb width <10% SL (Figure 17); longest lower jaw tooth 6.9-25.0% SL 2

2A. Anterior margin of vomer deeply concave (Figure 2); least outside width between frontals 9.1-17.8% SL (Figure 19); number of lower jaw teeth 46-142 (>60 in specimens 25 mm and larger) (Figure 20); escal bulb width 1.9-5.1% SL (<3% SL in specimens >50 mm SL) ..... *Melanocetus murrayi* Günther 1887

2B. Anterior margin of vomer nearly straight (Figure 1); least outside width between frontals 13.5-28.6% SL (Figure 19); number of lower jaw teeth 32-90 (Figure 20); escal bulb width 3.8-8.6% SL (>4% SL in specimens >50 mm SL) 3

3A. Longest lower jaw tooth 8.4-25.0% SL (Figure 21); esca with compressed posterior and (usually) anterior crests (Figure 25); distribution nearly cosmopolitan ..... *Melanocetus johnsoni* Günther 1864

3B. Longest lower jaw tooth 6.9-13.1% SL (Figure 21); esca without posterior or anterior crests (Figures 26, 27); distribution restricted to eastern tropical Pacific 4

4A. Number of lower jaw teeth 58-90 (Figure 22); escal bulb width 5.2-8.5% SL (Figure 23); illicium length 34.6-56.0% SL (Figure 24); escal bulb with a conical, distal prolongation occasionally pigmented on tip (Figure 26) ..... *Melanocetus polyactis* Regan 1925

4B. Number of lower jaw teeth 37-57 (Figure 22); escal bulb width 3.8-5.0% SL (Figure 23); illicium length 29.8-38.8% SL (Figure 24); escal bulb with a low, rounded distal prolongation usually darkly pigmented on tip (Figure 27) ..... *Melanocetus niger* Regan 1925

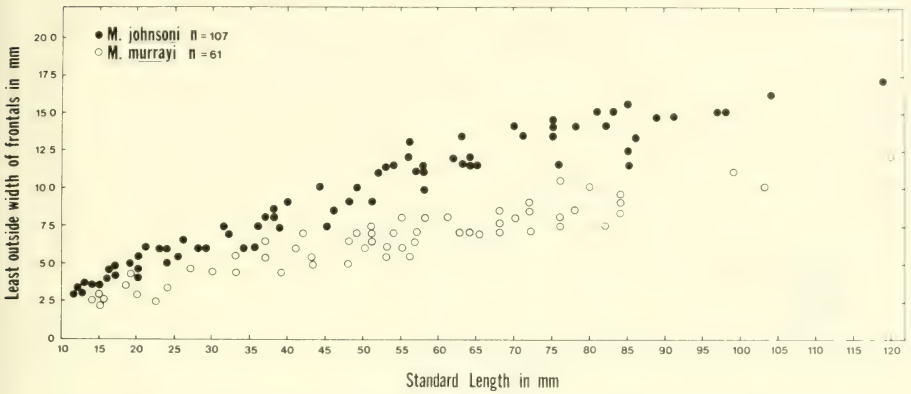


FIGURE 19.—Relationship between least outside width of frontals and standard length for two species of *Melanocetus*.

Melanocetus johnsoni Günther 1864
Figures 1, 3, 6, 16B, 17, 19-21, 25, 30, 31

Females

Melanocetus johnsoni Günther 1864:301-303, pl. 25 (original description, single specimen, holotype BMNH 1864.7.18.6, 64 mm, Madeira, 24 December 1863); Lütken 1871:64, 74 (comparison with *Oneirodes eschrichtii*); Lütken 1872:329-340, 343 (after Lütken 1871); Günther 1880:473, fig. 211 (after Günther 1864); Günther 1887:56-57 (after Günther 1864, comparison with *M. murrayi*); Vaillant 1888:346 (after Günther 1864); Goode and Bean 1896:494, fig. 406 (description after Günther 1864); Gill 1909:582, 584, 585, fig. 20 (after Günther 1864, Goode and Bean 1896); Regan 1912:286, fig. 6C (cranial osteology); Regan 1913:1096 (description of additional specimen, natural history); Regan 1926:18, 32, 33, fig. 10 (description of additional material, cranial osteology; *M. krechi* and *M. rotundatus* synonyms); Parr 1927:29 (description of additional specimen); Norman 1930:354 (additional record); Regan and Trewavas 1932:27-29, 49-52, fig. 19-21, 22A, B, 72, 73 (description of additional material, osteology, and esca figured, in key); Fowler 1936:1143, 1144, 1346, 1363 (description after Günther 1864, Regan 1926, Norman 1930); Norman 1939:114 (additional material); Koefoed 1944:3-5, pl. 1, fig. 1 (description of additional specimen, comparison with *M. murrayi*; Beebe and Crane 1947:152 (description of additional specimen, color); Fowler 1949:158-159 (listed); Bertelsen 1951:7, 40-41, 43-46, 48-53, fig. 13, 15, 17-19, tables 4, 6 (description of females, males, larvae, comparison with all known material, in key); Grey 1956:235-236 (synonymy; distribution); Monod 1960:687, fig. 80 (pectoral radials); Maul 1961:91-92, fig. 1 (description of additional material); Maul 1962a:6-7 (description, additional material); Struhsaker 1962:841-842 (description, additional specimen, skin spines); Bussing 1965:222 (additional specimen); Fitch and Lavenberg 1968:127, fig. 70 (distinguishing characters, natural history); Pietsch 1972a:29, 35, 36, 38, 45 (osteological comments); Maul 1973:667 (synonymy, after Bertelsen 1951).

Melanocetus krechi Brauer 1902:293-294 (original description, single specimen, holotype ZMHU 17688, 45 mm, *Valdivia* stn. 239, Indian Ocean, 5°42′ S, 43°36′ E, 0-2,500 m); Brauer 1906:319-320, pl. 15, fig. 1, 2 (description after Brauer 1902); Gill 1909:583, 584, fig. 21 (after Brauer

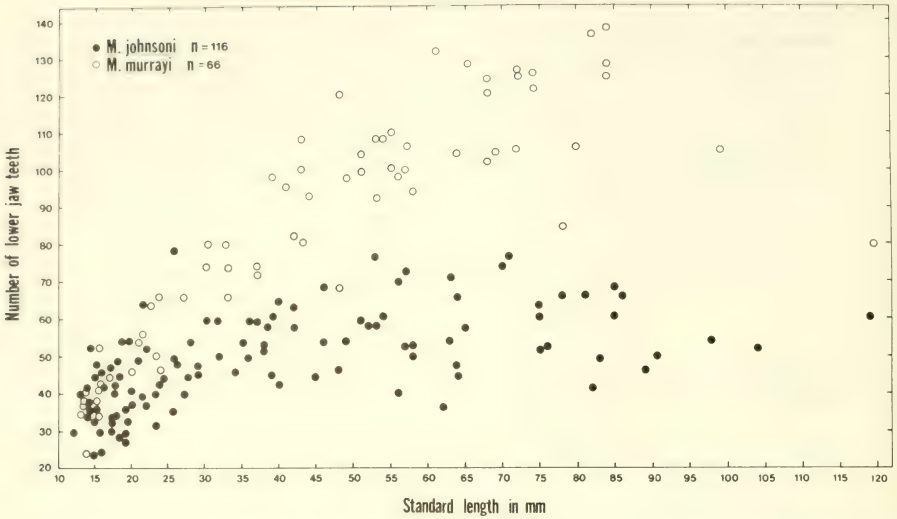


FIGURE 20.—Relationship between number of lower jaw teeth and standard length for two species of *Melanocetus*.

1902, 1906); Murray and Hjort 1912:87, 614 (in part, additional specimen, misidentification); Borodin 1931:84 (additional specimen, misidentification); Regan and Trewavas 1932:49, 52, fig. 74 (misidentification, in key); Fowler 1936: 1143, 1144 (description after Brauer 1902, 1906, in key); Bertelsen 1951:40, table 4 (comparison with all known material).

Melanocetus rotundatus Gilchrist 1903:206-208, pl. 15 (original description, two specimens, both lost [see Comments, p. 76], the largest about 28 mm, off Cape Point and Natal coast, South Africa, 1,098 m); Gilchrist and Thompson 1917:417 (after Gilchrist 1903); Barnard 1927:1007, pl. 37, fig. 5 (after Gilchrist 1903); Bertelsen 1951:48 (in synonymy of *M. johnsoni*).

Melanocoetus rotundatus, Smith 1949:429, fig. 1232 (after Gilchrist 1903); Penrith 1967:187, 188 (type material lost; a synonym of *M. johnsoni*).

Melanocetus ferox Regan 1926:33, pl. 9, fig. 1 (original description, single specimen, holotype ZMUC P9257, 78 mm, *Dana* stn. 1208(14), Gulf of Panama, 6°48′ N, 80°33′ W, 3,100 m wire, 1715 h, 16 January 1922); Regan and Trewavas 1932:49, 52, fig. 75 (in part, only holotype, additional material here referred to *M. polyactis*, in key); Beebe and Crane 1947:152 (in part, only holotype); Bertelsen 1951:44, 53, table 4 (in part, only holotype; comparison with all known material, in key); Grey 1956:237 (synonymy, distribution).

Melanocetus cirrifer Regan and Trewavas 1932:52-53, fig. 76A, 77, pl. 2, fig. 1 (original description, two females, lectotype ZMUC P9258, 25.5 mm, *Dana* stn. 3678(2), Banda Sea, 4°05′ S, 128°16′ E, 4,000 m wire, bottom depth 4,700 m, 1840 h, 24 March 1929, in key); Bertelsen 1951:44, 53, table 4 (description, comparison with all known material, in key); Grey 1956:237 (synonymy, distribution).

Melanocetus niger, Gregory 1933:400, fig. 272 (misidentification, osteology).

Melanocetus megalodontis Beebe and Crane 1947:152, fig. 1 (original description, single specimen, holotype CAS-SU 46488 [originally NYZS 25791], 25.5 mm, Templeton Crocker Expedition stn. 165 T-3, eastern tropical Pacific, 20°36′ N, 115°07′ W, 0-915 m, 17 May 1936); Bertelsen 1951:43, 48, table 4 (description, comparison with all known material, in key); Grey 1956:235 (synonymy, distribution); Mead 1958:133 (holotype passed to CAS).

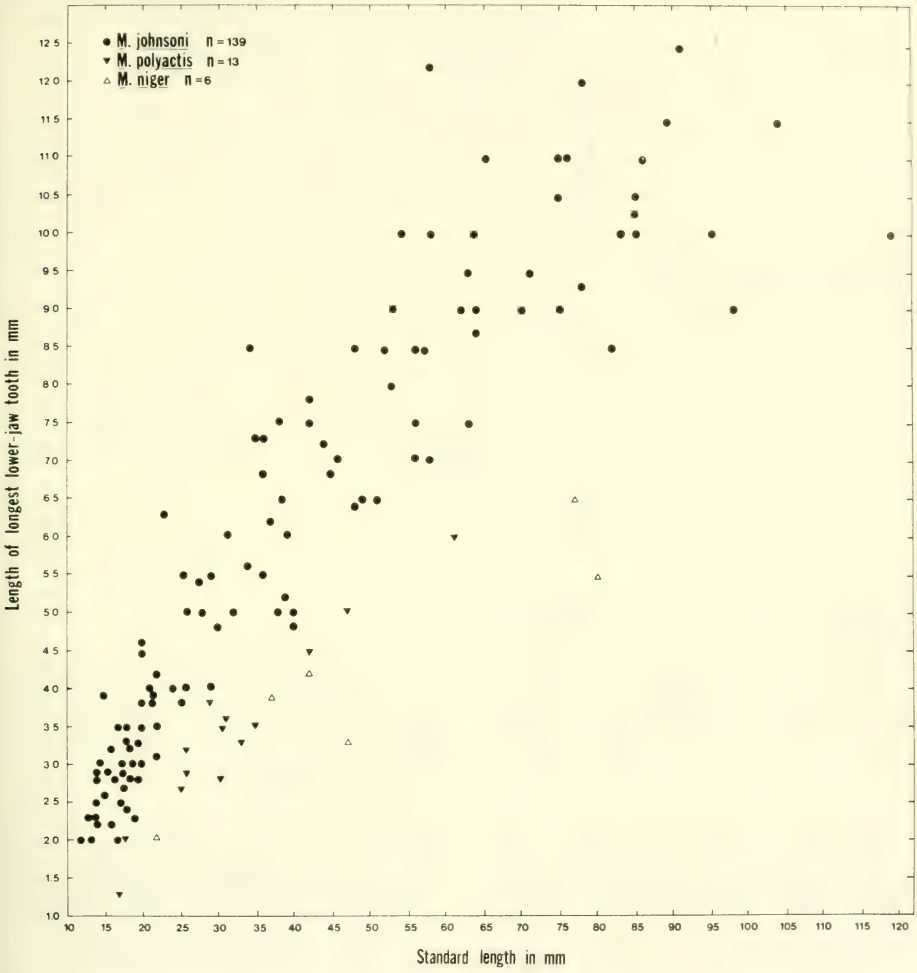


FIGURE 21.—Relationship between length of longest lower jaw tooth and standard length for three species of *Melanocetus*.

Melanocetus sp. Roule and Angel 1930:121, pl. 6, fig. 159 (additional material).

Males

Centrocetus spinulosus Regan and Trewavas 1932:53, 54, fig. 79 (original description, two specimens, lectotype ZMUC P9246, 15.5 mm, *Dana* stn. 3847(2), Indian Ocean, 12°02′ S, 96°43′ E, 3,000 m wire, bottom depth 2,825 m, 2100 h, 11 October 1929).

Xenoceratias macracanthus Regan and Trewavas 1932:11, 12 (erroneous spelling of specific name, listed).

Xenoceratias micracanthus Regan and Trewavas 1932:54, 55, fig. 81 (original description, single

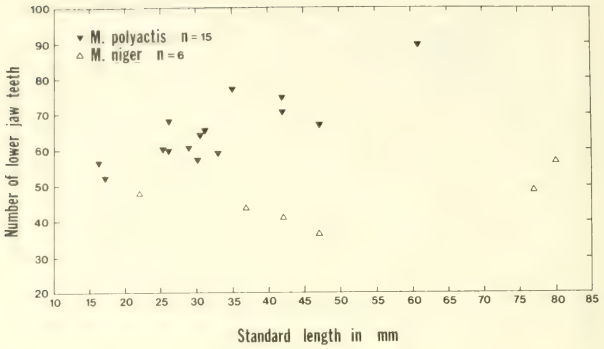


FIGURE 22.—Relationship between number of lower jaw teeth and standard length in two species of *Melanocetus*.

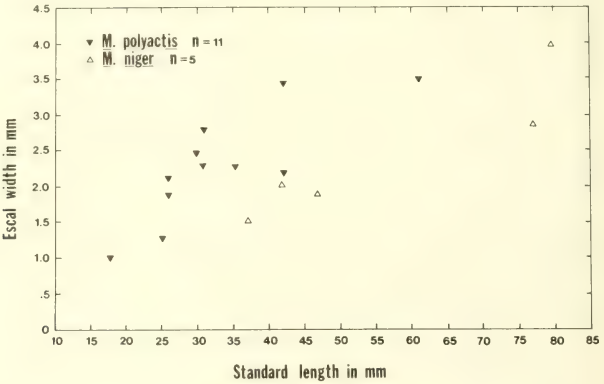


FIGURE 23.—Relationship between escal bulb width and standard length in two species of *Melanocetus*.

specimen, holotype ZMUC P9250, 28 mm, *Dana* stn. 4000(8), eastern tropical Atlantic, 0°31′ S, 11°02′ W, 4,000 m wire, bottom depth 3,750 m, 0630 h, 4 March 1930, in key); Fowler 1936:1364 (listed).

Xenoceratias heterorhynchus Regan and Trewavas 1932:54, 56, fig. 82 (original description, single specimen, holotype ZMUC P9248, 27 mm, *Dana* stn. 3716(2), South China Sea, 19°18.5′ N, 120°13′ E, 3,000 m wire, bottom depth 3,225 m, 1400 h, 22 May 1929, in key); Grey 1956:236 (synonymy, distribution).

Xenoceratias laevis Regan and Trewavas 1932:54, 57, fig. 83 (original description, single specimen, holotype ZMUC P9249, 23 mm, *Dana* stn. 3731(13), South China Sea, 14°37′ N, 119°52′ E, 2,000 m wire, bottom depth 2,300 m, 0200 h, 17 June 1929, in key).

Xenoceratias brevirostris Regan and Trewavas 1932:54, 57, fig. 84 (original description, single specimen, holotype ZMUC P9247, 19 mm, *Dana* stn. 3739(8), Celebes Sea, 3°20′ N, 123°50′ E, 3,000 m wire, bottom depth 4,475 m, 0700 h, 2 July 1929, in key).

Xenoceratias braueri Koefoed 1944:6, fig. 2 (original description, single specimen, holotype UBZM 4309, 18.5 mm, *Michael Sars* North Atlantic Deep-Sea Expedition stn. 53, central North Atlantic, 34°59′ N, 33°01′ W, 2,600 m wire, bottom depth 2,615-2,865 m, 8-9 June 1910).

Melanocetus johnsoni, Bertelsen 1951:44, 48-53, fig. 17C, D, F-H, table 6 (synonymy, distribution, comparison with all known material, in key); Grey 1956:236 (synonymy, distribution); Maul 1962b:36-37, fig. 2 (description of addi-

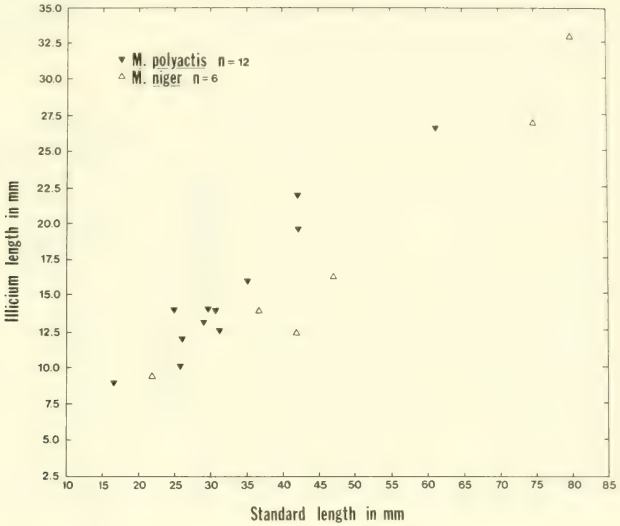


FIGURE 24.—Relationship between illicium length and standard length in two species of *Melanocetus*.

tional specimen); Maul 1973:667 (synonymy, after Bertelsen 1951).

Material. — Metamorphosed females, 346 (10-119 mm): AMS, 33 (11-88 mm); BMNH, 16 (13-64 mm); CAS, 1 (25.5 mm); FSM, 10 (13-76 mm); IOAN, 35 (12-75 mm); IOS, 7 (35-91 mm); ISH, 82 (15-119 mm); LACM, 65 (13.5-83 mm); MCZ, 25 (12-75 mm); NMNZ, 7 (12-55 mm); ROM, 4 (15-56 mm); SAM, 6 (10-13 mm); UMML, 3 (27-82 mm); USNM, 15 (12-85 mm); ZMUC, 37 (11.5-89 mm).

Diagnosis.—A species of *Melanocetus* unique in having the following combination of characters: anterior margin of vomer nearly straight (Figure 1); least outside width between frontals 13.5-28.6% SL (Figure 19); number of lower jaw teeth 32-78 (Figure 20), length of longest lower jaw tooth 8.4-25.0% SL (Figure 21); width of pectoral fin lobe 10.7-17.8% SL; escal bulb width 4.3-8.6% SL; illicium length 32.4-60.8% SL; esca with posterior and (usually) anterior crests (Figure 25); minute skin spines present over most of body; integument relatively thick (1.55 mm).

Description.—Escal bulb slightly compressed with a low, rounded or conical distal prolongation nearly always darkly pigmented on tip; a compressed posterior crest usually darkly pigmented, becoming larger and more conspicuous with growth; and a considerably smaller, compressed, anterior crest present in some specimens (Figure 25); integument relatively thick (cross sections measure 1.55 mm in thickness), not easily torn, usually retaining heavy pigmentation during fixation and preservation.

Number of upper jaw teeth 48-134; dorsal fin rays 13-15 (rarely 16), pectoral fin rays 17-22 (rarely 23) (Table 2).

Distribution. — *Melanocetus johnsoni* has a wide horizontal distribution in tropical and subtropical waters of all three major oceans of the world (see Distribution, p. 83). Compared with *M. murrayi*, it appears to occupy relatively shallow depths: about 62% of the material (for which data was available) was captured by open nets fished at maximum depths of 1,000 m; 82% of the material can be accounted for by gear fished above 1,500 m, and 98% by gear fished above 2,100 m (see Distribution, p. 83).

Comments. — *Melanocetus krechi* Brauer (1902) was synonymized with *M. johnsoni* by Regan (1926), resurrected by Regan and Trewavas (1932), and tentatively synonymized again with *M. johnsoni* by Bertelsen (1951). From the description and figure given by Brauer (1902, 1906)

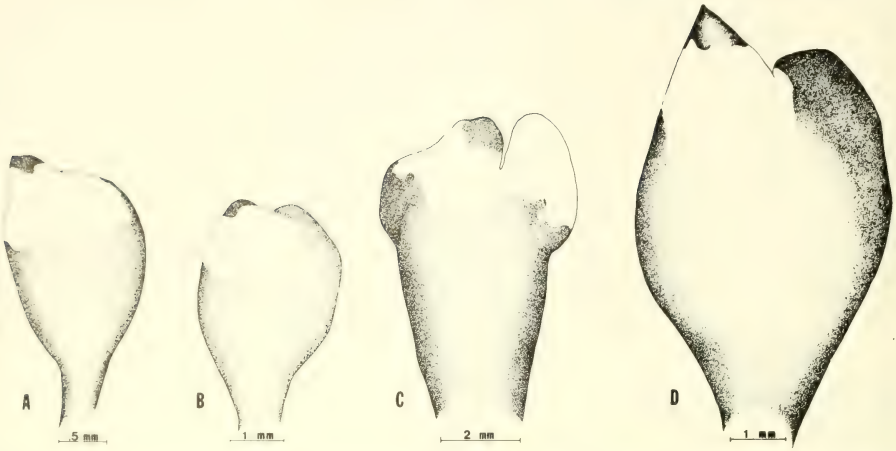


FIGURE 25.—Escae of *Melanocetus johnsoni*: A. ISH 1261/71, 21 mm SL; B. ISH 753/71, 38 mm SL; C. MCZ 49849, 75 mm SL; D. ISH 1534/71, 78 mm SL.

and based on a much greater knowledge of variation within the genus, there can be little doubt that this nominal form has been correctly placed within the synonymy of *M. johnsoni*.

Melanocetus ferox was described from a single specimen (78 mm) collected in the Gulf of Panama (Regan 1926). Two additional specimens of this nominal form were listed by Regan and Trewavas (1932). A thorough comparison of all known material led Bertelsen (1951, table 4) to suspect that *M. ferox* might represent individual variation of *M. niger*. The holotype of *M. ferox*, however, has relatively long lower jaw teeth (longest, 12.0% SL; Figure 21). In this, and in all other morphometric and meristic characters used here, it fits well within the material here recognized as *M. johnsoni*. Although the esca of the holotype is in poor condition, traces of a posterior crest remain. For these reasons *M. ferox* is synonymized with *M. johnsoni*. The two additional specimens identified as *M. ferox* by Regan and Trewavas (1932) (ZMUC P92210, 30.5 mm; BMNH 1932.5.3.6, 42 mm) have short jaw teeth; in this and in other ways they fit well within the material of *M. polyactis* (see p. 77).

Melanocetus cirrifer Regan and Trewavas (1932), described on the basis of two small females, was tentatively maintained by Bertelsen (1951) because of supposed differences in escal morphology and pigmentation which now can easily be shown to be part of the variation found within *M. johnsoni*. *Melanocetus megalodontis* Beebe and Crane (1947), based on a single specimen, was distinguished from all other species of the genus by ". . . the character of the illicium; in the great length and robustness of the fangs . . . and in the shortness of the lower jaw. . . ." However, specimens of *M. johnsoni* may have longer teeth and individuals of several species of *Melanocetus* may have as short a lower jaw (Bertelsen 1951, table 4). Further (as predicted by Bertelsen 1951), the "peculiar minute distal flaps" of the esca are artifacts. In all ways the holotype of *M. megalodontis* fits well within the variation now known to occur within *M. johnsoni*. Thus these nominal forms, *M. cirrifer* and *M. megalodontis*, are placed within the synonymy of *M. johnsoni*.

Finally, the holotype and paratype of *M. rotundatus* Gilchrist (1903) have been lost. The circumstances of their demise are the same as for the holotype of *Dolopichthys cornutus* described elsewhere (Pietsch 1972b; see also Barnard 1927, Penrith 1967). Although Gilchrist's (1903) original description is poor, the figure provided by him shows rather long jaw teeth, a long illicium bearing a relatively large escal bulb, and a large pectoral fin lobe. This combination of characters makes it nearly certain that *M. rotundatus* is a synonym of *M. johnsoni* (Penrith 1967).

Melanocetus polyactis Regan 1925
Figures 21-24, 26, 30

Females

Melanocetus polyactis Regan 1925:565 (original description, 3 specimens, lectotype designated by Bertelsen 1951, ZMUC P9260, 61 mm, *Dana* stn. 1206(3), Gulf of Panama, 6°40′ N, 80°47′ W, 3,500 m wire, 1845 h, 14 January 1922); Regan 1926:34, pl. 8, fig. 2 (description after Regan 1925); Regan and Trewavas 1932:53, fig. 78 (listed, after Regan 1925, 1926); Bertelsen 1951:44, 54-55, tables 4, 7, 8 (description, additional material, 2 males, 6 larvae, comparison with all known material, in key); Grey 1956:238 (synonymy, distribution).

Melanocetus niger Regan 1925:565 (in part, 3 of 11 cotypes [see Comments, p. 79], all Gulf of Panama); Regan 1926:33, pl. 8, fig. 1 (in part, description, 4 additional specimens); Regan and Trewavas 1932:53, fig. 76B (in part, listed, after Regan 1925, 1926); Bertelsen 1951:44, 53, table 4 (in part, description, comparison with all known material, in key); Grey 1956:237 (in part, synonymy, distribution).

Melanocetus ferox, Regan and Trewavas 1932:49, 52, fig. 75 (in part, nontype material only, in key); Bertelsen 1951:44, 53, table 4 (in part, nontype material only, comparison with all known material, in key); Grey 1956:237 (in part, after Bertelsen 1951, synonymy, distribution).

Males

Rhynchoceratias rostratus, Regan 1926:44 (in part, misidentification).

Rhynchoceratias leucorhinus, Regan 1926:44 (in part, misidentification).

Material. — Metamorphosed females, 15 (16.5-61 mm): BMNH 1925.8.11.30, 26 mm; BMNH 1925.8.11.32, 42 mm (paralectotype); BMNH 1932.5.3.6, 42 mm; IOAN uncatalogued, 33 mm; LACM 33603-4, 2 (16.5 and 30 mm); LACM 33574-5, 17 mm; LACM 33624-1, 33 mm; LACM 33629-3, 35 mm; ZMUC P92155, 25 mm (paralectotype); ZMUC P921974, 26 mm; ZMUC P9251, 29 mm; ZMUC P92210, 30.5 mm; ZMUC P9253, 47 mm; ZMUC P9260, 61 mm (lectotype).

The following adolescent females, all collected from the eastern tropical Pacific, are only tentatively referred to *M. polyactis*: LACM 33618-2, 16 mm; LACM 31119-2, 2 (17 and 18 mm); LACM 31109-2, 18 mm; LACM 31120-20, 2 (18 and 19 mm); LACM 31126-29, 2 (19.5 and 20 mm).

Metamorphosed males, 2: ZMUC P92460, 16 mm (22 mm total length (TL)); ZMUC P92459, 19.5 mm (30 mm TL).

Larvae, 6 (2 males, 4 females, 3-9 mm TL): ZMUC P92461; ZMUC P92462.

Diagnosis. — A species of *Melanocetus* unique in having the following combination of characters: anterior margin of vomer nearly straight; least outside width between frontals 18.0-26.0% SL; number of lower jaw teeth 58-90 (Figure 22); length of longest lower jaw tooth 9.3-13.1% SL (Figure 21); width of pectoral fin lobe 10.9-16.0% SL; escal bulb width 5.2-8.5% SL (Figure 23); illicium length 34.6-56.0% SL (Figure 24); esca with a conical, distal prolongation, crests absent (Figure 26); integument relatively thick.

Description. — Escal bulb not compressed, with conical distal prolongation nearly always slightly constricted at base, and usually as long as or longer than length of escal bulb, pigmented on tip in some specimens, posterior and anterior crests absent (Figure 26); integument as in *M. johnsoni*.

Number of upper jaw teeth 42-120; dorsal fin rays 14-17; pectoral fin rays 17-21 (rarely 22 and 23) (Table 2).

Distribution. — *Melanocetus polyactis* appears to be restricted to the eastern tropical Pacific Ocean where 15 specimens have been collected between lat. 10° N and 13° S as far west as long. 88° W (see Distribution, p. 83). Approximately 67% of the material was captured by open nets fished at maximum depths of 1,000 m or below.

Comments. — *Melanocetus polyactis* is most easily confused with *M. niger*. Both forms are similar in having exceptionally short lower jaw teeth (Figure 21). They differ significantly, however, in the number of lower jaw teeth, escal bulb width, and illicial length (see Key, Figures 22-24).

Part of the material originally listed as *M. niger* has been reallocated to *M. polyactis* (see Comments, p.79). Also included with the material of *M. polyactis* are two specimens (ZMUC P92210, 30.5 mm; BMNH 1932.5.3.6, 42 mm) previously identified as *M. ferox* by Regan and Trewavas (1932).

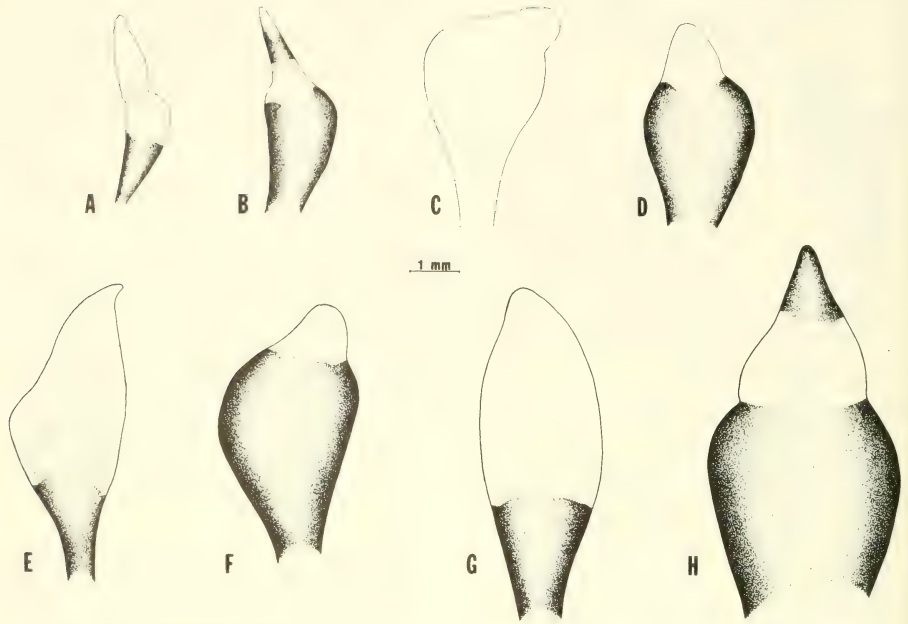


FIGURE 26.—Escae of *Melanocetus polyactis*: A. LACM 33603-4, 16.5 mm SL; B. Paralectotype, ZMUC P92155, 25 mm SL (lack of distal pigmentation probably due to abrasion); C. ZMUC P921974, 26 mm SL; D. ZMUC P9251, 29 mm SL (a cotype of *M. niger*); E. LACM 33603-4, 30 mm SL; F. ZMUC P92210, 30.5 mm SL; G. LACM 33629-3, 35 mm SL; H. Lectotype, ZMUC P9260, 61 mm SL.

Melanocetus niger Regan 1925
Figures 21-24, 27, 30

Melanocetus niger Regan 1925:565 (original description, in part, 4 of 11 cotypes [see Comments, p. 79] all Gulf of Panama, lectotype hereby designated, ZMUC P9252, 80 mm, *Dana* stn. 1208(4), 6°48′ N, 80°33′ W, 3,500 m wire, 0810 h, 16 January 1922); Regan 1926:33, pl. 8, fig. 1 (in part, description, 4 additional females); Regan and Trewavas 1932:53, fig. 76B (in part, listed after Regan 1925, 1926); Beebe and Crane 1947:153-154 (in part, description of 4 additional females not seen by us); Bertelsen 1951:44, 53, table 4 (in part, description, comparison with all known material, in key); Grey 1956:237 (in part, synonymy, distribution).

Material. — Metamorphosed females, 6 (22-80 mm): BMNH 1925.8.11.29, 47 mm (paralectotype); IOAN uncatalogued, 77 mm; ZMUC P9254, 22 mm (paralectotype); ZMUC P9256, 37 mm (paralectotype); ZMUC P921973, 42 mm (*Galathea* stn. 727); ZMUC P9252, 80 mm (lectotype).

Males and larvae unknown.

Diagnosis. — A species of *Melanocetus* unique in having the following combination of characters: anterior margin of vomer nearly straight; least outside width between frontals 14.3-24.3% SL; number of lower jaw teeth 37-57 (Figure 22); longest lower jaw tooth 6.9-10.5% SL (Figure 21); width of pectoral fin lobe 9.1-13.5% SL; escal bulb width 3.8-5.0% SL (Figure 23); illicium length 29.8-38.8% SL (Figure 24); esca without crests (Figure 27); integument relatively thick.

Description. — Escal bulb not compressed, with a low, rounded or conical distal prolongation nearly always pigmented on tip; anterior and posterior

crests absent (Figure 27); integument as in *M. johnsoni*.

Number of upper jaw teeth 29-86; dorsal fin rays 14-15; pectoral fin rays 18-21 (Table 2).

Distribution. — All six known specimens of *M. niger* were collected in the Gulf of Panama and adjacent waters of the eastern tropical Pacific Ocean as far west as approximately long. 90° W (see Distribution, p. 83). Eighty-three percent of the material was captured by open nets fished at maximum depths of 1,500 m and below.

Comments. — *Melanocetus niger* was briefly described by Regan (1925) from seven specimens collected in the Gulf of Panama without type designation and without a listing of individual sizes, station numbers, or other means of identification. Regan (1926) added four more specimens without providing means of separating the original seven. All 11 specimens bear labels indicating cotype status and all are treated here as part of the original type material. One of these is designated the lectotype (ZMUC P9252, 80 mm), three are referred to *M. polyactis* (BMNH 1925.8.11.30, 26 mm; ZMUC P9251, 29 mm; ZMUC P9253, 47 mm), three unidentifiable specimens are listed below as *Melanocetus* sp. (ZMUC P9255, 13.5 mm; BMNH 1925.8.11.31, 14 mm; BMNH 1925.8.11.28, 43 mm), and one is unaccounted for and presumed lost (*Dana* stn. 1209(3), 37 mm total length). The remaining three specimens are recognized as paralectotypes of *M. niger*.

Melanocetus eustalus n. sp.
Figures 18, 28, 30

Melanocetus ferox, Pietsch 1972b:10 (misidentification, luminescence); Brewer 1973:25 (after Pietsch 1972b, distribution).

Melanocetus sp. Pietsch 1976:782, 783 (reproduction).

Material. — A single female, the holotype, LACM 30037-12, 111 mm, *Velero IV* stn. 11748, eastern Pacific off Mazatlán, Sinaloa, Mexico, 21°39′ N, 106°58′ W, 3 m IKMT, 0-1,675 m, bottom depth 2,820 m, 1320-2136 h, 11 November 1967.

Diagnosis. — A species of *Melanocetus* unique in having the following combination of characters: anterior margin of vomer nearly straight; least outside width between frontals 18.0% SL; number of lower jaw teeth 60; longest lower jaw tooth 5.9% SL; illicium length 30.6% SL; width of pectoral fin lobe 9.9% SL; escal bulb width 11.3% SL; esca without crests (Figures 18, 28); integument relatively thick.

Description of holotype. — Escal bulb large (length 14.4% SL), slightly compressed, with a low conical distal prolongation, pigment absent; pos-

FIGURE 27.—Escae of *Melanocetus niger*: A. Paralectotype, ZMUC P9256, 37 mm SL; B. Paralectotype, BMNH 1925.8.11.29, 47 mm SL; IOAN uncatalogued, 77 mm SL; D. Lectotype, ZMUC P9252, 80 mm SL.

terior and anterior crests absent (Figure 28); integument as in *M. johnsoni*.

Gill opening exceptionally large, greatest diameter 23.4% SL; number of upper jaw teeth 91; vomerine teeth 8; dorsal fin rays 15; pectoral fin rays 16 (Table 2).

Etymology. — The name *eustalus* is derived from the Greek *eustales*, an adjective meaning well equipped, in reference to the enormous esca of this ceratioid.

Luminescence. — Upon capture, the holotype of *Melanocetus eustalus* was maintained alive for several minutes during which the bulb of the esca glowed continuously with a bright, golden-orange light. The amount of light actually emitted, however, appeared to be controlled by an up and down

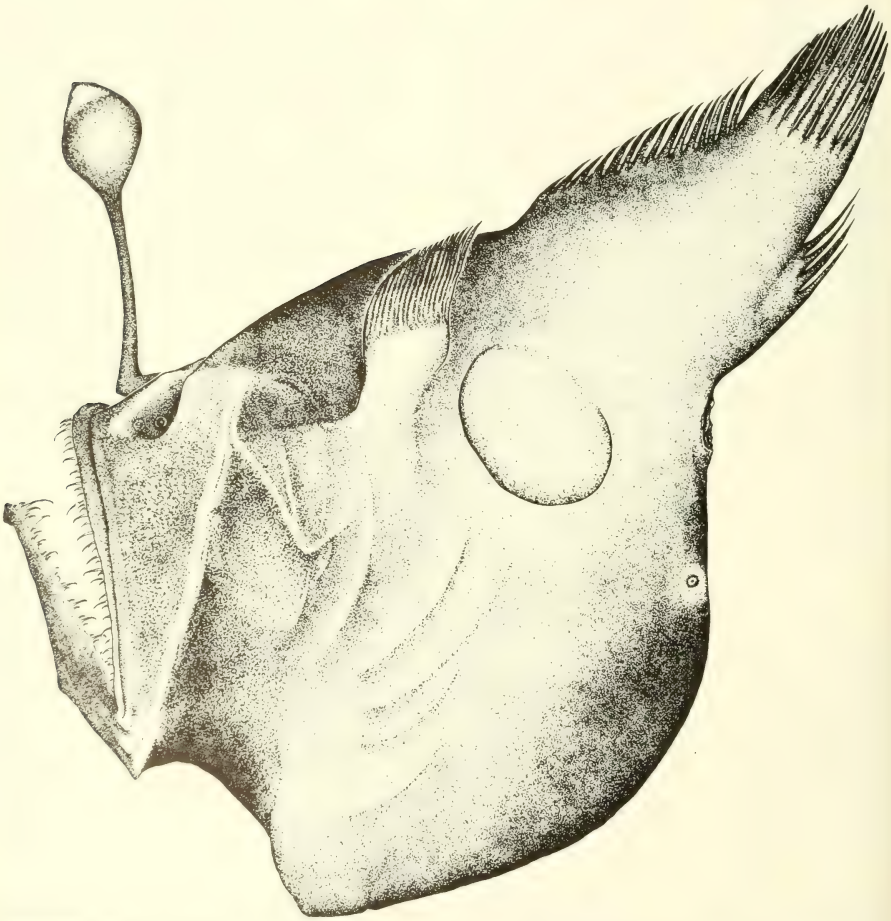


FIGURE 28.—Holotype of *Melanocetus eustalus*, LACM 30037-12, 111 mm SL, lateral view. Drawn by Elizabeth Anne Hoxie.

movement of the darkly pigmented, inner wall of the photophore of the esca. The glowing bulb was almost entirely covered and uncovered four or five times within a period of at least 1 min (B. G. Nafpaktitis[3]; see Pietsch 1972b). A mechanism of this kind would provide a rapid means of extinguishing light that may not only attract potential mates and prey, but also predators.

Melanocetus murrayi Günther 1887
Figures 2, 4, 5, 7-15, 16A, 19, 20, 29-31

Females

Melanocetus murrayi Günther 1887:57, pl. 11, fig. A (original description, two specimens, lectotype BMNH 1887.12.7.17, 71 mm, *Challenger* stn. 106, central Atlantic, 1°47′ N, 24°26′ W, 0-3,386 m); Regan 1926:32 (description, additional material, in key); Parr 1927:27 (description, additional material); Regan and Trewavas 1932:27, 49-50, fig. 22C, 23, 71 (description, additional material; pectoral radials, pelvic bone, escae figured; in key); Beebe 1932:99-102, fig. 29, 30 (description of postlarvae); Parr 1934:7 (listed); Fowler 1936:1143, 1144-1145, 1346, 1363, fig. 483 (after Günther 1887; Regan 1926; in key); Koefoed 1944:3, 5 (description, comparison, additional material); Fowler 1949:158 (listed); Bertelsen 1951:40-48, fig. 16, tables 4, 5 (description of females, males, larvae, comparison with all known material, in key); Grey 1955:299 (additional material, color); Grey 1956:234 (synonymy; distribution); Monod 1960:687, fig. 80 (pectoral radials); Pietsch 1972a:34, 38 (osteological comments); Maul 1973:667 (synonymy, after Bertelsen 1951).

Melanocetus bispinosus Günther 1880:473 (name only); Goode and Bean 1896:495 (in synonymy).

Melanocetus (Liocetus) murrayi Günther 1887:56 (original description, a distinct subgenus).

Liocetus murrayi, Goode and Bean 1896:495, fig. 407 (new combination, after Günther 1887); Gill 1909:583, 584, fig. 22 (after Günther 1887; Goode and Bean 1896).

Melanocetus vorax Brauer 1902:294 (original description, single specimen, holotype ZMHU 17710, 85 mm, *Valdivia* stn. 63, Gulf of Guinea, 2°00′ N, 8°04′ W, 0-2,492 m); Brauer 1906:320-321, pl. 15, fig. 4 (description after Brauer 1902). Fowler 1936:1143, 1144 (description after Brauer 1902, 1906; in key).

Melanocetus johnsoni, Brauer 1906:319 (misidentification); Regan 1926:33 (in part, misidentification); Murray and Hjort 1912:609, 614, 618, fig. 469 (misidentification); Fowler 1936, fig. 482 (figure after Brauer 1906).

Melanocetus krechi, Murray and Hjort 1912:614, 618 (in part, misidentification).

Melanocetus tumidus Parr 1927:28-29, fig. 10 (original description, single juvenile, holotype BOC 2022, 15 mm, *Pawnee* Third Oceanographic Expedition stn. 11, western North Atlantic, 23°58′ N, 77°26′ W, 2,135 m wire, 2 March 1927); Regan and Trewavas 1932:49 (mentioned); Grey 1956:239 (synonymy, distribution, a young female *M. murrayi*).

Melanocetus niger, Parr 1927:29 (misidentification); Beebe 1929:18 (misidentification).

Males

Rhynchoceratias acanthirostris Parr 1927:31, fig. 11 (original description, single specimen, holotype BOC 2011, 20 mm, *Pawnee* Third Oceanographic Expedition stn. 22, western North Atlantic, 23°37′ N, 77°15′ W, 2,135 m wire, 12 March 1927); Parr 1930b:130, 134 (anatomy, life history).

Rhynchoceratias latirhinus Parr 1927:32, 33, fig. 12 (original description, single specimen, holotype BOC 2012, 15 mm, *Pawnee* Third Oceanographic Expedition stn. 33, western North Atlantic, 24°11′ N, 75°37′ W, 2,440 m wire, 22 March 1927).

Rhynchoceratias longipinnis Parr 1930a:7, fig. 2-5 (original description, single specimen, holotype BOC 2592, 16 mm, *Pawnee* Third Oceanographic Expedition stn. 59, Bermuda, 32°19′ N, 64°32′ W, 2,440 m wire, 21 April 1927, osteology); Parr 1930b:129, fig. 1-3, 6, 7 (anatomy, life history).

Xenoceratias acanthirostris, Regan and Trewavas 1932:54, 55 (new combination; description after Parr 1927, in key).

Xenoceratias longipinnis, Regan and Trewavas 1932:54, 56 (new combination; description after Parr 1927, in key).

Xenoceratias latirhinus, Regan and Trewavas 1932:54, 57 (new combination; description after Parr 1927, in key).

[3]B. G. Nafpaktitis, Professor, Department of Biological Sciences, University of Southern California, Los Angeles, CA 90007, pers. commun. November 1967.

Xenoceratias regani Koefoed 1944:4, 6, pl. 1, fig. 6 (original description, single specimen, holotype UBNM 4311, 20 mm, *Michael Sars* North Atlantic Deep-Sea Expedition stn. 53, central North Atlantic, 34°59′ N, 33°01′ W, 2,600 m wire, bottom depth 2,615-2,865 m, 8-9 June 1910).

Melanocetus murrayi, Bertelsen 1951:44-48, fig. 16A, D, F, H, table 5 (synonymy, description, comparison with all known material, in key); Grey 1956:235 (synonymy, distribution); Maul 1962b:37-38, fig. 3 (description of additional specimen); Maul 1973:667 (synonymy, after Bertelsen 1951).

Material.—Metamorphosed females, 140 (13.5-120 mm): BMNH, 8 (21-57 mm); BOC, 1 (15 mm); CAS, 3 (14.5-51 mm); FSM, 6 (13.5-54 mm); IOAN, 5 (14-56 mm); IOS, 6 (17-68 mm); ISH, 33 (15-120 mm); LACM, 14 (13-84 mm); MCZ, 14 (13-84 mm); UMML, 28 (17-99 mm); USNM, 7 (15-78 mm); VIMS, 1 (33 mm); ZMUC, 14 (14-80 mm).

Diagnosis. — A species of *Melanocetus* unique in having the following combination of characters: anterior margin of vomer deeply concave (Figure 2); least outside width between frontals 9.1-17.8% SL (Figure 19); number of lower jaw teeth 46-142 (Figure 20); longest lower jaw tooth 7.7-16.7% SL; width of pectoral fin lobe 6.1-8.9% SL; escal bulb width 1.9-5.1% SL; illicium length 23.1-37.2% SL; esca with crests minute or absent (Figure 29); minute skin spines restricted to caudal peduncle; integument relatively thin (0.48 mm).

Description. — Escal bulb not compressed, with a low, rounded distal prolongation usually unpigmented on tip; posterior and anterior crests minute or absent (Figure 29); integument thin, easily torn (cross sections measure 0.48 mm in thickness), pigment readily lost during fixation and preservation, often transparent, especially in gill region and over branchiostegal rays.

Number of upper jaw teeth 34-178; dorsal fin rays 12-14, pectoral fin rays 15-19 (rarely 20) (Table 2).

Distribution. — *Melanocetus murrayi* has a wide horizontal distribution in the Atlantic and Pacific, but is apparently absent from the Indian Ocean (see Distribution, p. 83). Compared with *M. johnsoni*, it is a much deeper living form: only 10% of the material (for which data was available) was captured in open nets fished at maximum depths of <1,000 m. Approximately 58% of the material was taken by gear fished at maximum depths of 1,500 m or below, and 45% by gear fished at 2,000 m or below (see Distribution, p. 83). The relatively thin integument of *M. murrayi* (less than one-third the thickness of that of its congeners) as well as a lighter, less well-ossified skeleton reflects the poorer trophic economies of these greater depths (see Description above).

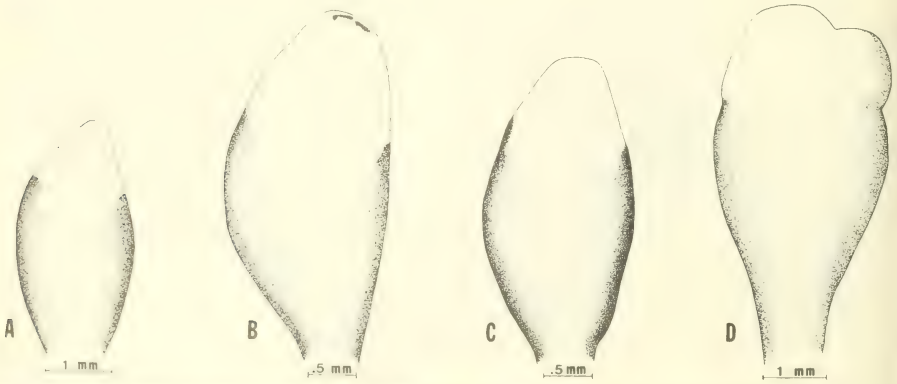


FIGURE 29.—Escae of *Melanocetus murrayi*: A. ISH 2961[illegible] SL; B. ISH 922/68, 70 mm SL; C. ISH 2961/71, 76 mm SL; D. ISH [illegible] mm SL.

Comments. — *Melanocetus vorax* Brauer (1902) was tentatively synonymized with *M. murrayi* by Regan (1926). This decision was confirmed by Regan and Trewavas (1932) and later by Bertelsen (1951). *Melanocetus tumidus* Parr 1927 (not mentioned by Bertelsen 1951) was based on a single metamorphosing female (15 mm) that fits well within the larval and metamorphosing material of *M. murrayi* (Bertelsen 1951) in lacking pigment on the caudal peduncle and having a faintly pigmented gill cover. This nominal form is hereby synonymized with *M. murrayi*.

Species Incertae Sedis

The following two nominal species based on males are distinguished from other *Melanocetus* males in having the posterior nostril well separated from the eye. They are probably not specifically distinct from each other and are most likely the males of one of the above recognized species based on females (Bertelsen 1951, fig. 20).

Melanocetus longirostris (Regan and Trewavas 1932) Incertae Sedis

Xenoceratias longirostris Regan and Trewavas 1932:54, 55, fig. 80 (original description, single specimen, holotype ZMUC P9259, 21 mm, *Dana* stn. 3751(7), north of New Guinea, 3°40′ N, 137°53′ E, 3,000 m wire, 1240 h, 12 July 1929); Fowler 1936:1346 (after Regan and Trewavas 1932; type species designation).

Melanocetus longirostris, Bertelsen 1951:42-44, 54 (new combination, comparison with all known material, in key); Grey 1956:238 (synonymy, distribution after Bertelsen 1951).

Melanocetus nudus (Beebe and Crane 1947) Incertae Sedis

Xenoceratias nudus Beebe and Crane 1947:155, text fig. 2 (original description, single specimen, holotype CAS-SU 46495 [originally NYZS 28402], 21.5 mm, Eastern Pacific *Zaca* Expedition stn. 210T-8, south of Cape Blanco, Costa Rica, 9°12′ N, 85°10′ W, 915 m, 27 February 1938).

Melanocetus nudus Bertelsen 1951:43-44, 54, fig. 20 (new combination, description of one additional specimen, comparison with all known material, in key); Grey 1956:238 (synonymy, distribution after Bertelsen 1951).

Melanocetus species

The following females, all considered to be part of the original type material of *M. niger* (see Comments, p. 79), are so poorly preserved that they cannot be referred to any described species of the genus: BMNH 1925.8.11.31, 14 mm; ZMUC P9255, 13.5 mm; BMNH 1925.8.11.28, 43 mm (illicium absent).

The following males cannot be satisfactorily identified to species based on females. Variation in the number of denticular teeth and pectoral fin rays and in the subdermal pigmentation (Bertelsen 1951) is considerably greater than previously thought (see Diagnosis of family above): LACM, 73 (11.5-24 mm) (66 from Hawaii at lat. 21°20-30′ N, long. 158° 20-30′ W; 3 from the Banda Sea; 2 from the Mid-American Trench at approximately lat. 18° N, long. 104° W; and 2 from the Equator at about long. 170° E and 145° W).

DISTRIBUTION

The family Melanocetidae is widely distributed throughout all three major oceans of the world in a broad belt limited by the Arctic and Antarctic Polar Fronts, with northern and southernmost records at approximately lat. 62° N and 46° S. It is present in the Gulf of Mexico, but has not been collected in the Gulf of California or the Mediterranean Sea (Figure 30).

Two of the five species of the family are wide ranging forms: *M. johnsoni* occurs throughout the Atlantic, Pacific, and Indian Oceans; *M. murrayi* is found throughout the Atlantic and Pacific Oceans but has so far not been recorded from the Indian Ocean. Two lesser known species, *M. polyactis* and *M. niger*, are restricted to the eastern tropical Pacific Ocean. *Melanocetus eustalus* is represented by a single specimen collected in the eastern Pacific off Mazatlán, Sinaloa, Mexico.

Since the majority of collections of melanocetids were made with nonclosing nets, the actual depth of capture is unknown. Furthermore, because sample sizes are small a statistical treatment of the nonclosing net data is impossible. Assuming, however, that most specimens were caught at depths where gear is fished for the longest period of time, vertical distributions may be roughly estimated by referring to the maximum depth reached by gear for each capture. On this assumption, members of the Melanocetidae may be taken anywhere between 250 m and some unknown

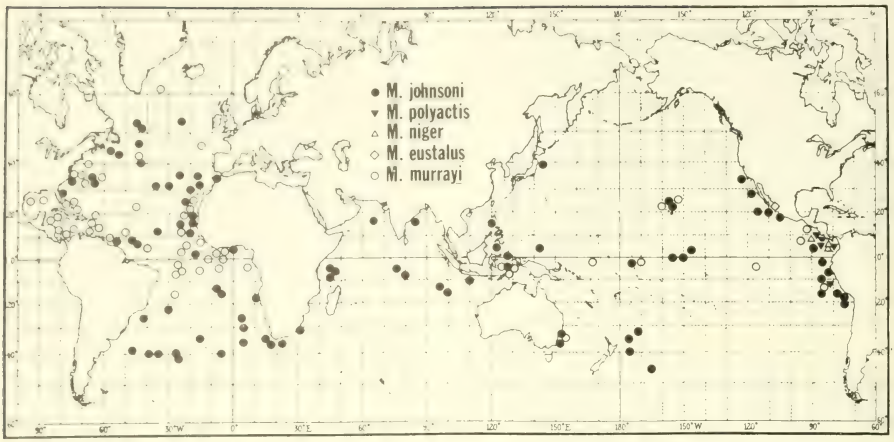


FIGURE 30.—Geographical distribution of *Melanocetus* species. Symbols may indicate more than one capture.

lower depth limit exceeding 3,000 m, but they are commonly found between roughly 500 and 2,500 m. *Melanocetus johnsoni* is most often collected between 500 and 1,500 m. *Melanocetus murrayi* is a considerably deeper dwelling species; the bulk of the known material was collected between 1,000 and 2,500 m (Figure 31). The relatively thin integument (see Description above) and lighter, less well-ossified skeleton of *M. murrayi* reflects the poorer trophic economies of these greater depths. The remaining species of the genus are so poorly represented in collections that their vertical distributions cannot be estimated.

EVOLUTIONARY RELATIONSHIPS

The Melanocetidae appears to be a relatively underived ceratioid family (Bertelsen 1951; Pietsch 1972a, 1976, 1979). The five species are characterized by a confusing mosaic of primitive and derived character states such that an interpretation of interspecific phylogenetic relationships is difficult. In any case, however, it seems apparent that *M. murrayi* has split off from the main line of melanocetid evolution and acquired a number of unique features that reflect its most derived position in the genus: 1) depressed cranium, 2) concave vomer, 3) small pectoral fin, 4) tiny escal bulb, and 5) thin integument. Living in considerably deeper strata than its congeners most probably also reflects a derived condition.

The four remaining species are much more closely related to each other than any is to *M. murrayi*. Five characters can be used to distinguish these forms: 1) number of lower jaw teeth, 2) longest lower jaw tooth, 3) illicium length, 4) escal bulb width, and 5) escal morphology. Unfortunately, all but the last of these characters overlap in variation among the remaining forms of the genus, and, furthermore, the relative primitiveness of character states among these features is nearly impossible to determine. *Melanocetus johnsoni* is perhaps derived in having a relatively long illicium, and in having fewer, but longer jaw teeth (see Pietsch 1972b, 1974, 1975). *Melanocetus polyactis* and *M. niger* are similar in having relatively short jaw teeth, a similar escal morphology lacking anterior and posterior crests, and a sympatric geographic distribution that is restricted to the Gulf of Panama and adjacent eastern tropical Pacific. *Melanocetus eustalus* is derived in having an extremely large escal bulb, comparable with no other known ceratioid.

ACKNOWLEDGMENTS

We thank E. Bertelsen for critically reading the manuscript and offering valuable suggestions. The following people and institutions provided study material: John R. Paxton (AMS), Alwyne Wheeler (BMNH), William N. Eschmeyer (CAS), Carter Gilbert (FSM), N. V. Parin (IOAN), Nigel

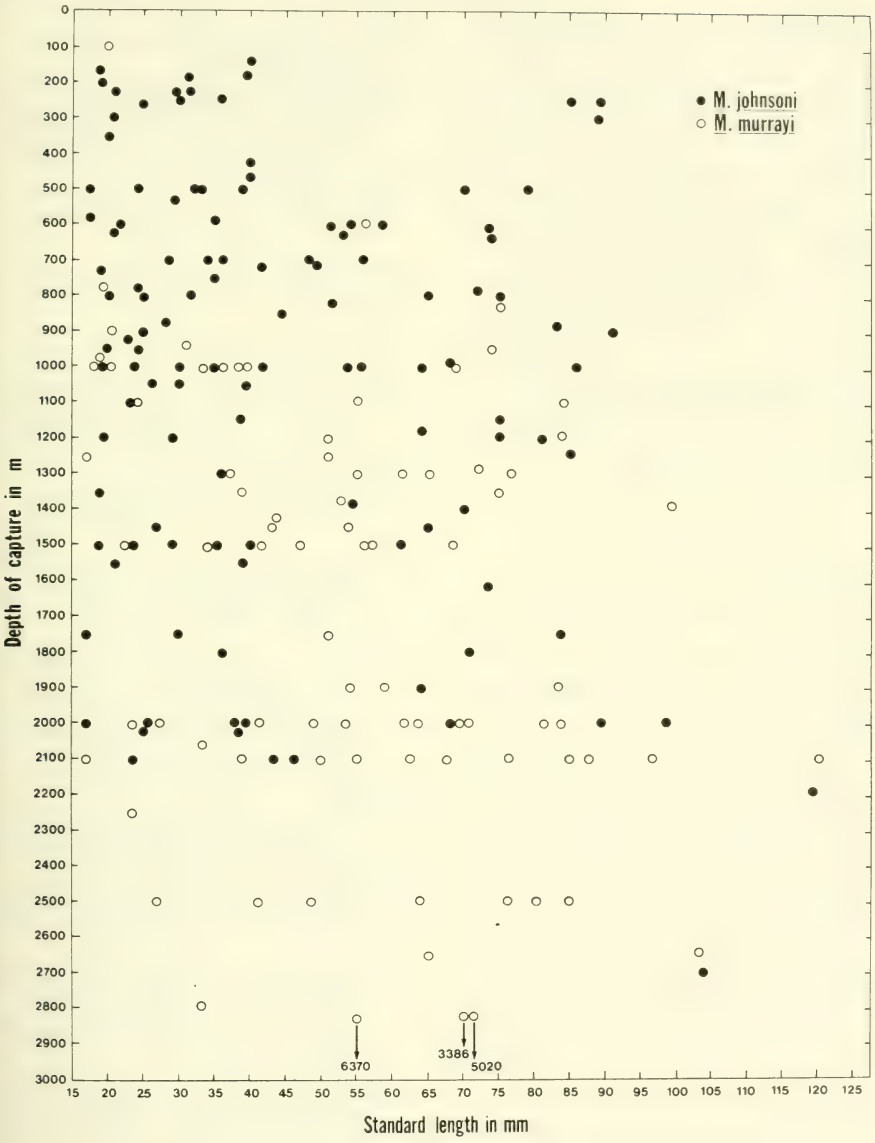


FIGURE 31.—Relationship between depth of capture (based on maximum depth reached by fishing gear) and standard length for two species of *Melanocetus*.

Merrett (IOS), Gerhard Krefft and Alfred Post (ISH), Robert J. Lavenberg and Jerry W. Neumann (LACM), Karsten Hartel (MCZ), Jack Moreland and C. D. Paulin (NMNZ), Allen Emery (ROM), P. A. Hulley (SAM), C. Richard Robins (UMML), Robert H. Gibbs and Susan Karnella (USNM), E. Bertelsen (ZMUC), Thomas A. Clarke (Hawaii Institute of Marine Biology), Richard E. Young (University of Hawaii at Manoa), Brett Stephenson (Auckland Museum, New Zealand), and Don A. Robertson (Ministry of Agriculture and Fisheries, Wellington, New Zealand). Elizabeth Anne Hoxie provided Figures 17, 18, and 28. The work was supported by National Science Foundation Grants GB-40700, DEB 76-82279 and DEB 7826540, the National Geographic Society, and PHS Biomedical Research Support Grant No. RR-07096 administered through the Graduate School Research Fund of the University of Washington.

LITERATURE CITED

BARNARD, K. H.
1927. A monograph of the marine fishes of South Africa. Part II. Ann. S. Afr. Mus. 21:419-1065.

BEEBE, W.
1929. Deep sea fish of the Hudson Gorge. Zoologica (N.Y.) 12:1-19.
1932. Nineteen new species and four post-larval deep-sea fish. Zoologica (N.Y.) 13:47-107.

BEEBE, W., AND J. CRANE.
1947. Eastern Pacific Expeditions of the New York Zoological Society. XXXVII. Deep-sea ceratioid fishes. Zoologica (N.Y.) 31:151-182.

BERTELSEN, E.
1951. The ceratioid fishes. Ontogeny, taxonomy, distribution, and biology. Dana Rep. Carlsberg Found. 39, 276 p.

BORODIN, N. A.
1931. Atlantic deep-sea fishes. Bull. Mus. Comp. Zool. Harvard Coll. 72(3):55-89.

BRADBURY, M. G.
1967. The genera of batfishes (family Ogcocephalidae). Copeia 1967:399-422.

BRAUER, A.
1902. Diagnosen von neuen Tiefseefischen, welche von der Valdivia-Expedition gesammelt sind. Zool. Anz. 25:277-298.
1906. Die Tiefsee-Fische. I. Systematischer Teil. Wiss. Ergeb. Dtsch. Tiefsee-Exped. Dampfer "Valdivia" 15, 432 p.

BREWER, G. D.
1973. Midwater fishes from the Gulf of California and the adjacent Eastern Tropical Pacific. Nat. Hist. Mus. Los Ang. Cty., Contrib. Sci. 242, 47 p.

BUSSING, W. A.
1965. Studies of the midwater fishes of the Peru-Chile Trench. *In* G. A. Llano (editor), Biology of the Antarctic Seas II. Am. Geophys. Union Res. Ser. 5:185-227.

FITCH, J. E., AND R. J. LAVENBERG.
1968. Deepwater teleostean fishes of California. Univ. Calif. Press, Berkeley, 155 p.

FOWLER, H. W.
1936. The marine fishes of West Africa, based on the collection of the American Museum Congo Expedition, 1909-1915. Bull. Am. Mus. Nat. Hist. 70:607-1493.
1949. The fishes of Oceania—Supplement 3. Mem. Bernice P. Bishop Mus. 12:37-186.

GILCHRIST, J. D. F.
1903. Description of new South African fishes. Mar. Invest. S Afr. 2:203-211.

GILCHRIST, J. D. F., AND W. W. THOMPSON.
1917. Catalogue of the fishes of Natal. Ann. Durban Mus. 1(4):255-431.

GILL, T.
1909. Angler fishes: Their kinds and ways. Smithson. Inst., Annu. Rep. 1908:565-615.

GOODE, G. B., AND T. H. BEAN.
1896. Oceanic ichthyology, a treatis on the deep-sea and pelagic fishes of the world, based chiefly upon the collections made by the steamers *Blake*, *Albatross*, and *Fish Hawk* in the northwestern Atlantic. U.S. Natl. Mus. Spec. Bull. 2, 553 p.

GREGORY, W. K.
1933. Fish skulls, a study of the evolution of natural mechanisms. Trans. Am. Philos. Soc. 23:75-481.

GRAY, M.
1955. Notes on a collection of Bermuda deepsea fishes. Fieldiana Zool. 37:265-302.
1956. The distribution of fishes found below a depth of 2000 meters. Fieldiana Zool. 36:75-337.

GÜNTHER, A.
1864. On a new genus of pediculate fish from the sea of Madeira. Proc. Zool. Soc. Lond. 1864:301-303.
1880. An introduction to the study of fishes. Adams and Charles Black, Edinburgh, xvi + 720 p
1887. Report on the deep-sea fishes collected by H.M.S. *Challenger* during the years 1873-1876. Rep. Sci. Res. Voy. Challenger, Zool. 22, 335 p.

KOEFOED, E.
1944. Pediculati from the "Michael Sars" North Atlantic Deep-Sea Expedition 1910. Rep. Sci. Res. "Michael Sars" North Atl. Deep-Sea Exped. 1910 IV, 2(1), 18 p.

LE DANOIS, Y.
1964. Étude anatomique et sytématique des antennaires, de l'ordre des Pédiculates. Mém. Mus. Natl. Hist. Nat., Ser. A, Zool. 31, 162 p.

LÜTKEN, CHR.
1871. *Oneirodes eschrichtii*, Ltk. en ny grøndsk Tudsefisk. Overs K. Dan. Vidensk. Selsk. Forh. 1871:56-74.
1872. On *Oneirodes eschrichtii*, Lütken, a new lophioid fish from Greenland. Ann. Mag. Nat. Hist., Ser. 4, 9:329-344.

MAUL, G. E.
1961. The ceratioid fishes in the collections of the Museum Municipal do Funchal (Melanocetidae, Himantolophidae, Oneirodidae, Linophrynidae). Bol. Mus. Munic. Funchal 14(50):87-159.
1962a. On a small collection of ceratioid fishes from off Dakar and two recently acquired specimens from stomachs of *Aphanopus carbo* taken in Madeira (Melanocetidae, Himantolophidae, Diceratiidae,

Oneirodidae, and Ceratiidae). Biol. Mus. Munic. Funchal 16(54):5-27.

1962b. Report on the fishes taken in Madeiran and Canarian waters during the summer-autumn cruises of the "Discovery II" 1959 and 1961. I. The ceratioid fishes (Melanocetidae, Himantolophidae, Oneirodidae, Gigantactinidae, Linophrynidae). Bol. Mus. Munic. Funchal 16(56):33-46.

1973. Gigantactinidae. *In* J. C. Hureau and T. Monod (editors), Check-list of the fishes of the north-eastern Atlantic and of the Mediterranean, Vol. 1, p. 675. Unesco, Paris.

MEAD, G. W.

1958. A catalog of the type specimens of fishes formerly in the collections of the Department of Tropical Research, New York Zoological Society. Zoologica (N.Y.) 43:131-134.

MONOD, T.

1960. A propos du *pseudobrachium* des *Antennarius* (Pisces: Lophiiformes). Bull. Inst. Fr. Afr. Noire 22, Ser. A, 2:620-698.

MURRAY, J., AND J. HJORT.

1912. The depths of the ocean. A general account of the modern science of oceanography based largely on the scientific researches of the Norwegian steamer *Michael Sars* in the North Atlantic. Macmillian and Co. Ltd., Lond., 821 p.

NORMAN, J. R.

1930. Oceanic fishes and flatfishes collected in 1925-1927. Discovery Rep. 2:261-370.

1939. Fishes. Sci. Rep. John Murray Exped. 7:1-115.

PARR, A. E.

1927. Scientific results of the third Oceanographic Expedition of the "Pawnee" 1927. Ceratioidea. Bull. Bingham Oceanogr. Collect Yale Univ. 3(1):1-34.

1930a. On the osteology and classification of the pediculate fishes of the genera *Aceratias*, *Rhynchoceratias*, *Haplophryne*, *Laevoceratias*, *Allector* and *Lipactis*, with taxonomic and osteological description of *Rhynchoceratias longipinnis*, new species, and a special discussion of the rostral structures of the Aceratiidae. Occas. Pap. Bingham Oceanogr. Collect. 3, 23 p.

1930b. On the probable identity, life-history and anatomy of the free-living and attached males of the ceratioid fishes. Copeia 1930:129-135.

1934. Report on experimental use of a triangular trawl for bathypelagic collecting. Bull. Bingham Oceanogr. Collect, Yale Univ. 4(6), 59 p.

PENRITH, M. J.

1967. Ceratioid angler-fishes from South Africa. J. Nat. Hist. 1967:185-188.

PIETSCH, T. W.

1972a. A review of the monotypic deep-sea anglerfish family Centrophrynidae: taxonomy, distribution and osteology. Copeia 1972:17-47.

1972b. Ergebnisse der Forschungsreisen des FFS "Walter Herwig" nach Sudamerika, XIX. Systematics and distribution of ceratioid fishes of the genus *Dolopichthys* (family Oneirodidae) with the description of a new species. Arch. Fischereiwiss. 23:1-28.

1974. Osteology and relationships of ceratioid anglerfishes of the family Oneirodidae, with a review of the genus *Oneirodes* Lütken. Nat. Hist. Mus. Los Ang. Cty., Sci. Bull. 18, 113 p.

1975. Systematics and distribution of ceratioid anglerfishes of the genus *Chaenophryne* (family Oneirodidae). Bull. Mus. Comp. Zool. 147:75-100.

1976. Dimorphism, parasitism and sex: Reproductive strategies among deepsea ceratioid anglerfishes. Copeia 1976:781-793.

1979. Systematics and distribution of ceratioid anglerfishes of the family Caulophrynidae with the description of a new genus and species from the Banda Sea. Nat. Hist. Mus. Los Ang. Cty., Contrib. Sci. 310, 25 p.

REGAN, C. T.

1912. The classification of the teleostean fishes of the order Pediculati. Ann. Mag. Nat. Hist. Ser. 8, 9:277-289.

1913. A deep-sea angler-fish, *Melanocetus johnsonii*. Proc. Zool. Soc. Lond. 1913:1096-1097.

1925. New ceratioid fishes from the N. Atlantic, the Caribbean Sea, and the Gulf of Panama, collected by the "Dana." Ann. Mag. Nat. Hist., Ser. 9, 15:561-567.

1926. The pediculate fishes of the suborder Ceratioidea. Dana Oceanogr. Rep. 2, 45 p.

REGAN, C. T., AND E. TREWAVAS.

1932. Deep-sea angler fishes (*Ceratioidea*). Dana Rep. Carlsberg Found. 2, 113 p.

ROULE, L., AND F. ANGEL.

1930. Larves et Alevius de Poissons. Result. Campagnes Sci., Monaco 79:119-123.

SMITH, J. L. B.

1949. The sea fishes of Southern Africa. Central News agency Ltd., Cape Town, 550 p.

STRUHSAKER, P.

1962. The ceratioid fish *Melanocetus johnsoni* off the southeastern coast of the United States and a morphological observation. Copeia 1962:841-842.

TAYLOR, W. R.

1967. An enzyme method of clearing and staining small vertebrates. Proc. U.S. Natl. Mus. 122(3596), 17 p.

VAILLANT, L.

1888. Poissons. *In* A. Milne-Edwards, Expéditions scientifiques du Travailleur et du Tailisman pendant les anees 1880, 1881, 1882, 1883. G. Masson., Paris, 406 p.

EARLY LIFE HISTORY OF PACIFIC MACKEREL, *SCOMBER JAPONICUS*

JOHN R. HUNTER AND CAROL A. KIMBRELL[1]

ABSTRACT

The early life history of Pacific mackerel, *Scomber japonicus*, is described from laboratory-rearing studies and examination of stomach contents of sea-caught larvae. At 19° C mackerel eggs hatched in 56 hours, larvae were 3.1 mm standard length with a dry weight of 0.04 mg of which 50% was yolk. First feeding occurred 46 hours after hatching; all larvae fed by 60 hours (age 2.5 days). Larvae were then 3.6 mm long with fully pigmented eyes and 10% of the yolk remaining. Starvation was irreversible if larvae were not fed before age 4.5 days. Metamorphosis (15 mm standard length) occurred in 24 days at 16.8° C to 16 days at 22.1° C. Larvae 3-5 days old consumed 87% of their body weight per day and had a mean gross growth efficiency in dry weight of 33%. Oxygen consumption was 6.1 μl O_2 per milligram dry weight per hour at 18° C and 11.4 μl O_2 per milligram dry weight per hour at 22° C. Swimming speeds ranged from 1.3 standard lengths per second for first-feeding larvae to 3.8 standard lengths per second for fish at metamorphosis. Fifty percent of the larvae were able to capture a prey when the width of the prey was 85% of the width of the mouth and 95% were able to do so when the prey was 57% of the width of the mouth. Cannibalism was common in rearing groups; at 8 mm standard length, 50% of the larvae became capable of feeding on other fish larvae and cannibalism ceased when schooling commenced. Chief food items of sea-caught larvae were stages of copepods; maximum food width increased rapidly with larval length and was equivalent to the maximum mouth width. Mean prey width was 38% of mouth width. The larger organisms, constituting half of the prey eaten, accounted for 85-90% of the total volume of food eaten.

The development and distribution of eggs and larvae of the western Pacific population of the Pacific mackerel, *Scomber japonicus*, has been described (Kramer 1960; Kramer and Smith 1970), but little information exists on growth, behavior, and physiology of the larval stages. Incubation times and other data are known for the Japanese population of *S. japonicus* (Watanabe 1970). This paper provides some of the information needed to characterize the early life history of Pacific mackerel, including incubation times, yolk absorption, onset of feeding, vulnerability to starvation, swimming and feeding behavior, food ration, and oxygen consumption.

METHODS

Laboratory Experiments and Sea Samples

Eggs were obtained from Pacific mackerel maintained in spawning condition in the laboratory and induced to spawn by hormone injection (Leong 1977). Effects of temperature on incubation time were determined by placing test tubes containing 10 eggs and 25 ml of seawater in a temperature block set to produce a temperature gradient of 11.1°-23.3°±0.2° C (2 SE (standard error)) (Lasker 1964). Hatched eggs were counted at 2-4 h intervals and time from fertilization to 50% hatch estimated. Rate of yolk absorption was determined at 19.4°±0.4° C by measuring the surface areas of the yolk-sac and oil droplet from tracings made with an optical comparator (Wolfson 1965). Six samples, each of 15-25, larvae were taken over the first 72 h after hatching.

To estimate the time of first feeding at 18.9°±0.3° C, groups of larvae without past feeding experience were transferred to a 100 l container containing 150 rotifers/ml (*Brachionus plicatilus*). Four hours later, they were removed and the percentage of larvae that fed and the mean number of rotifers in the gut were calculated. Eight groups of 10-39 larvae were tested at periods from 18 to 114 h after hatching.

A starvation-based mortality curve was established at 19.0°±0.3° C by starting with 1,000 eggs in each of two 200 l containers, and counting and removing dead larvae daily. The age was determined at which starvation became irreversible in first-feeding larvae. Seven hundred and fifty eggs were incubated in each of four 200 l tanks and the resulting larvae were fed for the first time at

[1]Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

Manuscript accepted October 1979.
FISHERY BULLETIN: VOL. 78, NO. 1, 1980.

ages 2.5, 3.5, 4.5, and 5.5 d. The percentage survival was determined on the eighth day. Larvae were fed rotifers (50/ml) on the first day of feeding, and rotifers and copepods (*Tisbe* sp.) thereafter.

Vulnerability of newly metamorphosed Pacific mackerel (mean length 16.7 mm SL (standard length)) to starvation was tested at 18.9°±0.2° C by transferring fish from the rearing container to containers without food. One group of fish was starved for 4 d, another for 5 d, and a third was fed *Artemia salina* nauplii. The two starved groups were fed at the end of the starvation period.

Tail beat frequency and amplitude of larval Pacific mackerel (3-5 mm SL) were determined for routine swimming and burst speeds by analysis of cine films taken at 100 frames/s using techniques described by Hunter (1972). Routine swimming speeds of larval mackerel, at 19° C, were measured by counting the number of squares crossed by a larva (3.7-6.6 mm SL) as it swam over a 1 cm grid on the bottom of the rearing tank for 9-153 s; a 3 cm grid was used for larger larvae (7.9-13.1 mm SL) with shorter observation times (3-46 s). The mean of 15-25 visual observations was used as an estimate of speed for the mean length of the larvae in the tank on the day of observation; speeds were adjusted for parallax caused by the difference in depth between the grid and the fish. Speeds of juveniles (>19 mm SL) were measured by timing the fish as they swam a measured distance (35-201 cm) around the perimeter of the rearing tank; in this case mean speeds were for individual fish and observation times ranged from 3 to 26 s.

The size at which Pacific mackerel larvae were capable of ingesting various prey was evaluated by placing them in a 110 l container with the prey and estimating the number that fed by examination of stomach contents. The type of prey, mean prey size, prey density, and duration of feeding respectively were: yolk-sac anchovy larvae, 2.7 mm SL, 8/l, 2 h; *A. salina* nauplii, 0.2 mm wide, 11/l, 4 h; and anchovy eggs, 0.67 mm wide, 10/l, 2 h. The mouth width, prey width, and standard length of the larvae were measured and percentage feeding success was estimated for size classes of larval length and mouth width. The number of fish per size class was >9. Size thresholds for 50% feeding success and 95% success were estimated by probit analysis (Finney 1952) and expressed as a function of mean larval length, or mean prey width/mean mouth width.

The sizes of food items eaten by Pacific mackerel larvae in the sea was determined by examination of the stomachs of 86 larvae taken in routine ichthyoplankton surveys along the California coast. We recorded the length of each larva and the number and maximum width of all identifiable food items (Arthur 1976; Shirota 1970).

Food requirements were estimated by feeding the rotifer *Brachionus plicatilis* to 3-5 d old Pacific mackerel larvae. Seven to eight samples of 9-16 larvae each were taken over each of three 12-h feeding days, the number of rotifers in the guts of each larva were counted, and the counts converted to equivalent dry weight using the conversion factor of 0.16 μg/rotifer (Theilacker and McMaster 1971). Daily changes in larval weight were estimated from mean standard lengths using a length-dry weight conversion given in the results. The rate of gastric evacuation for 4 mm SL larvae was measured. They were allowed to feed for 4 h and then transferred to a tank without food; samples of 13-16 larvae were taken at about hourly intervals until the stomachs were empty. The number of rotifers in stomachs were counted and converted to dry weight, and the rate of gastric evacuation was estimated in terms of dry weight. The daily ration was estimated from the mean stomach contents and the rate of gastric evacuation. Gross growth efficiency was estimated in terms of dry weight from the daily ration and weight gain over 24 h.

Metabolic requirements of Pacific mackerel larvae were estimated using a Warburg respirometer and standard manometric techniques (Umbreit et al. 1964) to measure oxygen consumption. One or more Pacific mackerel larvae were added to an 18 ml Warburg flask filled with 4.4-8.7 ml of filtered seawater (salinity 33.58-33.93‰). Larvae >0.06 mg dry weight were tested individually. Twenty-one tests were made at 18.0°C of larvae or groups of larvae ranging in length from 3.7 to 17.9 mm SL (0.038-12.74 mg) and 14 at 22.0° C, of larvae 3.2-10.5 mm SL (0.025-2.86 mg). Flasks were shaken at 102 times/min for 5 out of every 30 min; readings were taken after the first 2 h and continued for 150-360 min. At the end of a test, larvae in each flask were measured, rinsed in distilled water, oven dried to a constant weight, and weighed. Mean weight was obtained for fish tested in groups. All runs were made under normal room illumination, about 700 lx. Log_{10} oxygen consumption in microliters O_2 per hour was regressed on $\log_{10}$ body weight for the 18.0° and 22.0° C experiments. As the slopes were close to unity, oxygen consumption was expressed in microli-

ters per milligram per hour. Metabolic requirements were compared with daily ration by converting oxygen consumption and daily ration to calories (1 μl O_2 = 0.005 cal: one *Brachionus plicatilis* = 0.00085 cal, Theilacker and McMaster 1971).

Culture of Larvae

Seven groups of Pacific mackerel were reared to metamorphosis to determine growth rates and effects of temperature on growth. The rearing containers were black fiber glass, cylindrical tanks (122 cm in diameter × 36 cm deep). Culture volume increased during the rearing period from 200 to 400 l because of the addition of seawater containing food and algae. Tank temperature was controlled by a regulated water bath, and groups were reared at temperatures ranging from 16.8° to 22.1° C. Illumination at the water surface during the 12-h day was about 2,000 lx. Tanks were started with 3,000 eggs/group. Initially, larvae were fed laboratory-cultured *Brachionus plicatilis*. At age 5 d, laboratory-cultured copepodids and adult copepods (*Tisbe* sp.) were added; 200,000 copepods were added daily until metamorphosis. Initially 30 or more rotifers/ml were added for the first few days of feeding; thereafter the density of rotifers was allowed to decline. On a diet of rotifers alone, growth slowed after larvae reached 5 mm SL and few larvae survived longer than 15 d. Newly metamorphosed juveniles were fed live and frozen adult *A. salina* and minced squid (*Loligo opalescens*) and northern anchovy. From 1 to 6 l of algal culture, *Tetraselmis* sp. (300,000-500,000 cells/ml), were added daily to provide food for rotifers and copepods. Samples of 10 or more larvae were taken on alternate days for length measurements. Some samples were washed in distilled water, dried, and subsequently weighed to obtain a relation between length and dry weight.

RESULTS

Hatching, Onset of Feeding and Starvation

Eggs of Pacific mackerel are transparent spheres, ranging in diameter from 1.06 to 1.14 mm (Kramer 1960). Incubation times ranged from 33 h at 23° C to 117 h at 14° C (Figure 1); eggs did not hatch below 14° C. The curve for hatching time as a function of temperature for the western Pacific population (data from Watanabe 1970) appears to be the same as the one for the eastern Pacific population.

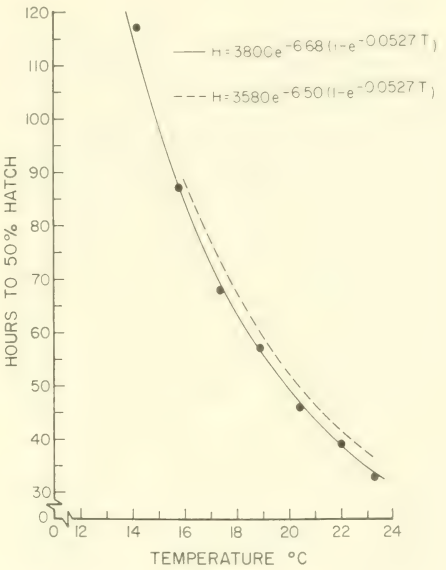


FIGURE 1.—Incubation time (fertilization to 50% hatch) of *Scomber japonicus* eggs. Solid line is for present data, points are estimated time to 50% hatch of eggs in five test tubes per temperature, dashed line is for data of Watanabe (1970). The general equation was developed by Zweifel and Lasker (1976) and fit to the 50% values.

At hatching, larvae averaged 3.1 mm SL (Figure 2B) and weighed 0.040 mg dry weight, of which 50% was yolk. At 19° C, first feeding occurred 46 h after hatching; by 60 h after hatching, all larvae had ingested one or more rotifers in 4 h (Figure 2D). Thus the 50% threshold for onset of feeding at 19° C occurred at about 50 h (2 d) after hatching. At this time larvae were 3.6 mm SL, the eyes were fully pigmented and 10% of the yolk remained, principally the remnants of the oil droplet (Figure 2A, B). Over the threshold for the onset of feeding, the mean number of rotifers in Pacific mackerel stomachs increased from 2 at 46 h to 14 at 68 h (Figure 2E). The larvae in each group had no previous feeding exposure, hence the increase in feeding activity with time could not be attributed to experience.

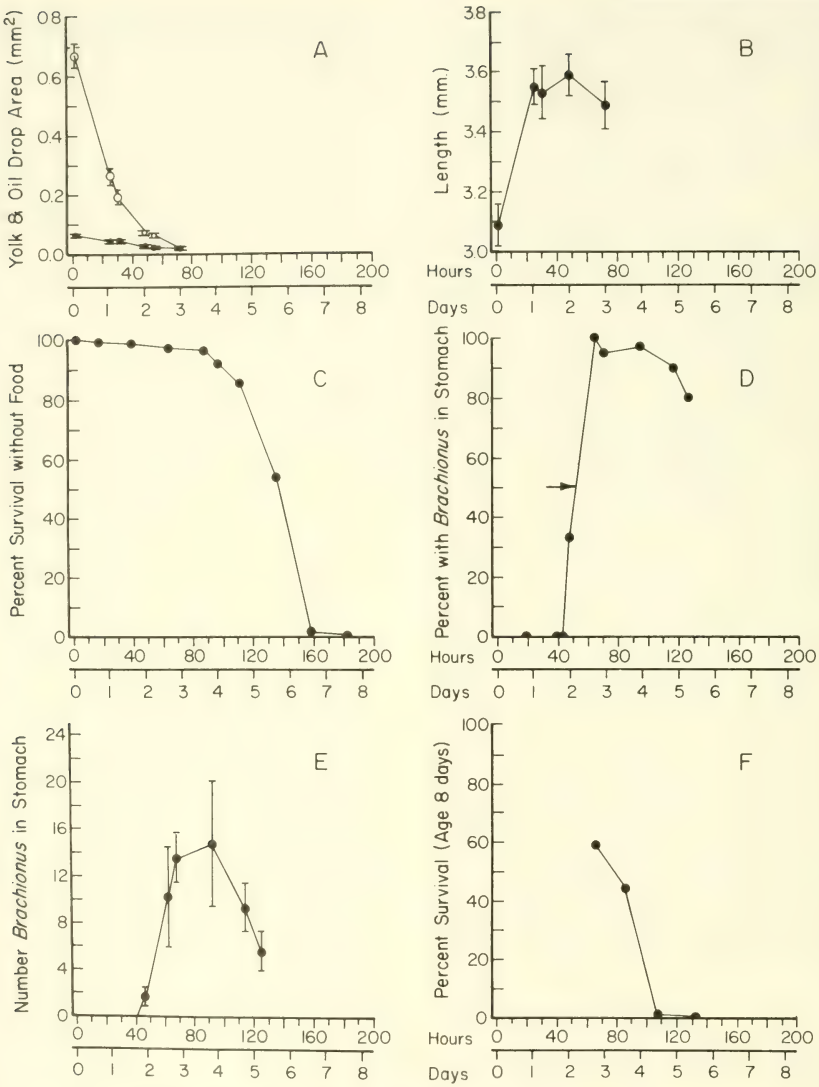


FIGURE 2.—Yolk absorption, onset of feeding, starvation, and point of irreversible starvation in Pacific mackerel larvae at 19° C: A. Rate of yolk absorption—open circles mean area of yolk-sac, solid circles mean area of oil droplet (mm^2). B. Mean length of larvae from hatching through yolk-absorption. C. Percent survival of larvae without food. D. Percent of larvae tested at various times after hatching that had ingested one or more *Brachionus plicatilis* in a 4-h test period—arrow indicates the 50% threshold for the onset of first feeding. E. Mean number of *B. plicatilis* per positive stomach of larvae tested at various times after hatching. F. Percentage survival at age 8 d for larvae fed for the first time at age 2.5, 3.5, 4.5, and 5.5 d—percentages are plotted at the time food was first added. Bars in A, B, and E represent ±2 SE of mean.

If larvae were not fed, most died between ages 4 and 7 d and none survived longer than 7 d (Figure 2C). Highest survival (on the eighth day after hatching) occurred when food was added for the first time at age 2.5 d; survival was somewhat lower if food was added at 3.5 d and negligible if added at 4.5 d (Figure 2F). Thus at 19° C starvation appeared irreversible if food was not provided before 4.5 d.

Pacific mackerel larvae, unlike herring or anchovy (Blaxter and Hempel 1963; Lasker et al. 1970), did not cease swimming or feeding at the time of irreversible starvation. At age 5 d, the incidence of larvae with rotifers in their stomachs was relatively high (80%) (Figure 2D), but the average number of rotifers per positive stomach was much less than in larvae fed first at age 2 or 3 d (Figure 2E). Thus at age 5 d, most larvae were still able to feed, but owing to their weakened condition, none were able to capture enough prey to survive.

Vulnerability of larvae to starvation persisted through metamorphosis. All juvenile Pacific mackerel appeared emaciated and swam slowly by the fourth day of starvation. Mortality of 10% occurred in the group starved 4 d; 50% mortality occurred in those fish starved 5 d. All juveniles surviving 4 and 5 d of starvation recovered when food was added; no mortality occurred in the controls. Thus, newly metamorphosed Pacific mackerel were able to withstand 1 or 2 d more of starvation than first-feeding larvae, but they were better able to recover from food deprivation.

Growth

Growth in length of Pacific mackerel larvae was slow and almost linear over the first 10-15 d until larvae reached about 6-7 mm SL; there followed a rapid acceleration through metamorphosis. We did not fit equations to these data because none of the standard growth equations gave a good fit to the entire growth curve. The effect of temperature on growth was not distinguishable over the initial growth period, but became obvious during the period of rapid growth (Figure 3, Table 1). To provide an index of the effect of temperature on growth, we expressed the duration of the larvae period (hatching to metamorphosis, 15 mm) as a function of temperature (inset in Figure 3). The Q_{10} was 3.0 when calculated from the equation in Figure 3 for the temperature range of our observations (16.8°-22.1° C).

The length-weight relation for Pacific mackerel larvae and juveniles is shown in Figure 4. The form of this equation was developed by James Zweifel and used by Hunter (1976) to express the length-weight relation for northern anchovy larvae. The curvilinear nature of the length-weight relation, still evident in the log-log plot (Figure 4), indicates that if a linear regression of $\log_{10}$ weight

TABLE 1.—Growth data (millimeters SL) for seven groups of *Scomber japonicus* larvae reared at different mean temperatures from hatching through metamorphosis.

Age (days)	22.1° C[1]			20.4° C			19.6° C			19.5° C			19.2° C			18.9° C			16.8° C		
	n	$\bar{x}$	SD	*n*	$\bar{x}$	SD	*n*	$\bar{x}$	SD	*n*	$\bar{x}$	SD	*n*	$\bar{x}$	SD	*n*	$\bar{x}$	SD	*n*	$\bar{x}$	SD
1										10	3.1	0.24							31	3.5	0.12
2	14	3.3	0.21	16	3.8	0.06	16	3.7	0.10	15	3.9	0.09	15	3.8	0.06						
3	14	3.5	0.30																		
4	10	3.6	0.22	18	3.8	0.26	33	4.2	0.23	10	4.0	0.17	15	4.0	0.20	10	3.7	0.20			
5																					
6	10	3.9	0.21	15	4.2	0.41	15	4.8	0.44	13	4.2	0.14	15	4.4	0.37	10	4.1	0.39	15	4.3	0.42
7										27	4.5	0.40									
8	12	4.5	0.55	15	5.7	0.77	15	6.0	0.39	25	4.7	0.56	15	5.0	0.40				15	5.1	0.43
9													5	5.9	0.13						
10	12	6.0	1.13	15	6.3	0.91	15	6.6	0.70	15	4.8	0.43	19	5.6	0.77	11	5.2	0.45			
11																			15	6.5	0.70
12	22	8.4	1.88	16	8.2	1.31	15	6.5	0.75	11	5.9	1.08	25	6.4	0.68	12	6.1	0.60	15	7.0	0.50
13																					
14	10	8.9	1.46	10	11.5	1.54	15	8.4	1.12	30	6.4	1.09	15	6.6	0.80				17	7.7	1.40
15																			11	8.1	1.08
16	10	14.9	1.45	15	14.1	2.01	15	8.9	1.76	16	8.5	2.21	15	7.1	0.81	13	7.6	1.50			
17										10	10.0	2.71				12	9.0	1.33	15	10.3	2.11
18				15	17.8	1.70	15	10.3	2.48				15	10.3	3.21	13	9.4	1.61	17	10.8	2.84
19	15	24.1	5.81																		
20							15	12.5	3.18	17	17.7	4.21	15	11.7	2.88				9	11.5	2.81
22							15	17.5	4.51				15	14.6	4.62						
23																15	13.7	1.26			
24							24	20.4	5.10				16	18.5	5.38	10	19.8	2.36			
25																			17	17.1	5.07

[1]Juvenile growth (age, *n*, $\bar{x}$, and (SD)): 26 d, 13, 34.4 mm (4.37); 29 d, 9, 43.9 mm (3.60); 39 d, 5, 55.0 mm (8.74); and 47 d, 9, 67.3 mm (10.30).

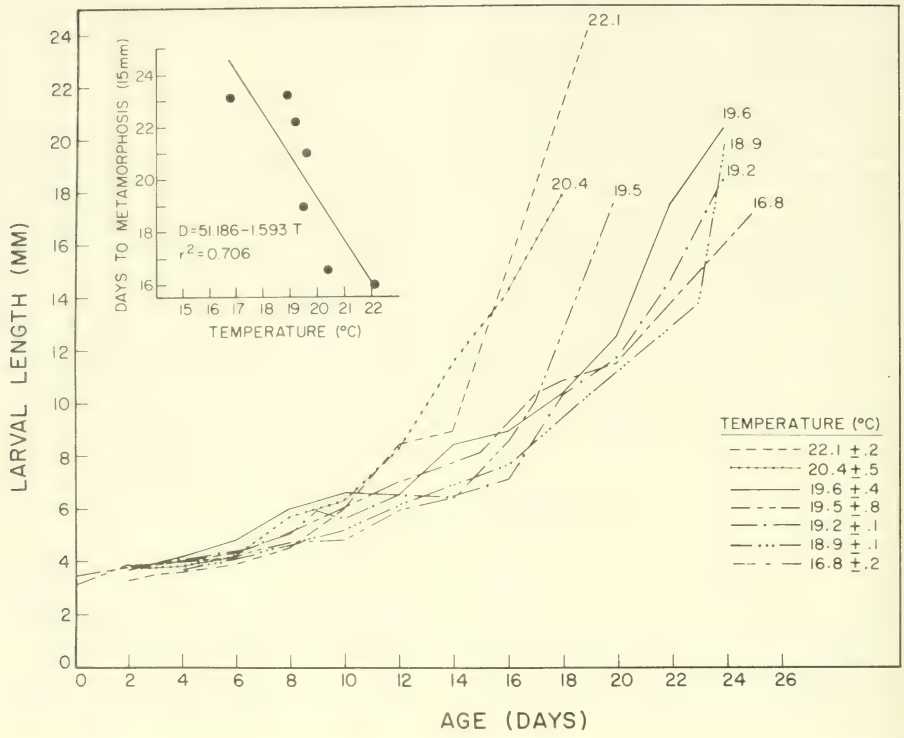


FIGURE 3.—Growth of seven groups of Pacific mackerel larvae reared in the laboratory from hatching (age 0 d) through metamorphosis (15 mm SL). Lines connect means given in Table 1; rearing temperatures (±2 SE) given on right side of figure and at end of lines. Inset at top: elapsed time (days) from hatching to metamorphosis (15 mm), as a function of rearing temperature.

on $\log_{10}$ length were used, it would produce inaccurate estimates.

Swimming Behavior

At typical cruising speeds, larval Pacific mackerel (3-5 mm SL) have a high tail beat frequency of about 30 beats/s and a low tail beat amplitude of 0.16 standard length. At slow speeds, tail beat frequency remained relatively constant but the amplitude of the tail beat changed. At higher speeds, both amplitude and frequency changed but the relative increase in amplitude was much greater than that of frequency (Table 2). Thus larval Pacific mackerel, unlike the adults (Hunter and Zweifel 1971), predominantly modulate tail beat amplitude to effect changes in speed.

Cruising speeds of Pacific mackerel increased markedly over the larval period from 0.46 cm/s (1.3 standard body lengths/s) for first-feeding larvae (3.6 mm SL) to 5.6 cm/s (3.8 standard body lengths/s) for fish at metamorphosis (Figure 5). This differs from the pattern in adult fishes where speed relative to size decreases with an increase in fish size (Webb 1975).

Feeding Behavior

Upon sighting a prey (rotifer or copepod), a Pacific mackerel larva advanced toward the prey,

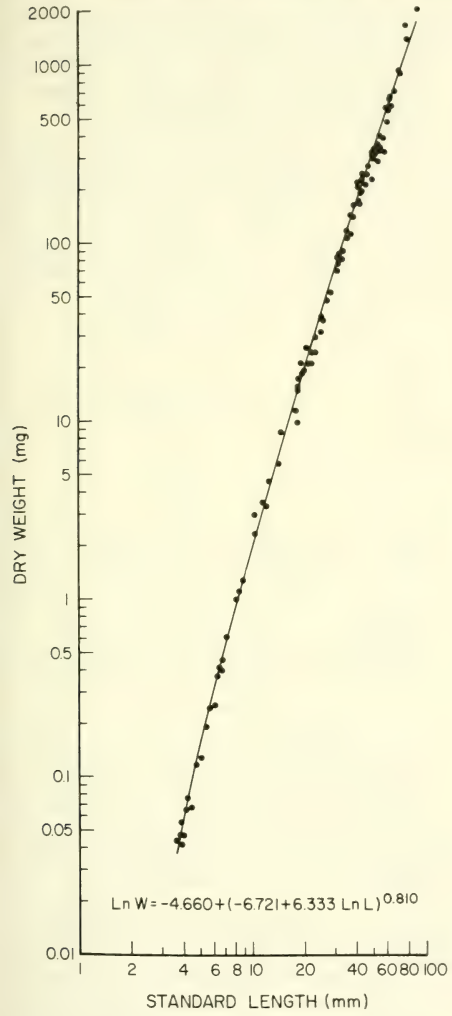


FIGURE 4.—Relation between dry weight (W) of larval and juvenile Pacific mackerel in milligrams and standard length (L) in millimeters. Points are observed values for individuals >18 mm and for larvae <18 mm; points are means for groups of 15 larvae.

stopped, drew back the tail, and held it in a slightly recurved, high amplitude position while the rest of the body remained relatively straight.

TABLE 2.—Tail beat frequency and amplitude and speed of 3-5 mm larval Pacific mackerel ($\bar{x}$ = 4.23±0.09 mm SL) expressed as a function of standard length.

N	Swimming speed (SL/s) Class interval	Mean	Tail beat Frequency (beats/s)	Tail beat Amplitude/SL
18	0.01- 1.0	0.58	33.2	0.12
30	1.01- 2.0	1.48	30.2	0.16
9	2.01- 3.0	2.48	30.2	0.17
3	3.1 - 5.0	4.00	37.5	0.18
3	10.1 -15.0	12.18	39.4	0.29
1	—	37.04	38.9	0.33

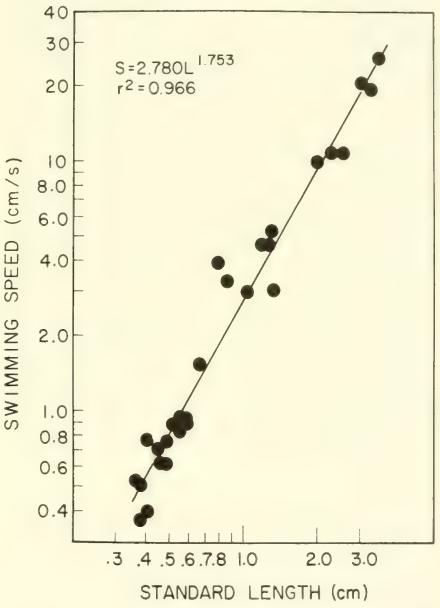


FIGURE 5.—Relation between swimming speed and standard length of Pacific mackerel larvae (log_{10} scales) at 19° C. Each point <2.0 cm is the mean of 15-25 observations. For ≥2.0 cm, individual fish were measured.

Feeding involved driving the tail posteriorly and opening the mouth. Larvae often attacked the same prey two or more times if the previous strike was unsuccessful, and repositioned for subsequent strikes by moving backward. Handling times were negligible because the prey was engulfed instantaneously. Older Pacific mackerel larvae developed a set of motor patterns for feeding on fish larvae; larvae were seized from the side and carried crosswise in the mouth. Larger prey were repeatedly released and grasped until they ceased

struggling, then released and ingested, usually head first. Handling times increased with prey size.

The length at which 50% of Pacific mackerel larvae were capable of capturing and ingesting anchovy yolk-sac larvae (LD_{50}, Finney 1952) was 8.1 mm SL (95% confidence interval, 7.2-9.5 mm) (Figure 6). Sibling cannibalism began when the mean length of the group was about 8 mm SL. At this size, the mean length of six cannibals was 10.8 mm SL (range 9.9-12.0 mm) and that of their prey was 6.2 mm SL (range 5.9-6.5 mm). Cannibalism in rearing containers ended as Pacific mackerel approached metamorphosis (15 mm SL) and schooling began. Rearing at higher temperatures increased the growth rate and thereby decreased the period over which sibling cannibalism occurred. Consequently, survival at metamorphosis was higher in groups reared at 20°-22° C (5-6%) than it was at 19° C or lower temperatures (1-2%).

Near metamorphosis, Pacific mackerel were able to eat relatively large fish larvae. Three Pacific mackerel, 15.4-16.0 mm SL, placed in a rearing tank with northern anchovy larvae (12.0-20.6 mm SL) captured and began to ingest larvae of 11.7-13.5 mm SL, within 6 min. Thus, as Pacific mackerel larvae grew from 8 mm SL to metamorphosis, the size of anchovy larvae, they were able to eat increased from about 3 to 13 mm SL. This increase in prey size was not closely related to mouth size of the Pacific mackerel because the mouth can be greatly expanded when ingesting a larval fish. Mouth size probably was inversely related to handling time as in the case for adult fishes (Kislalioglu and Gibson 1976).

When prey are engulfed rather than seized, mouth size may give a good indication of the size of prey a larvae is capable of ingesting. The relation between mouth width and length in Pacific mackerel larvae was slightly curvilinear, and mouth width increased from 0.216 mm for first-feeding larvae (3.6 mm SL) to 0.987 mm at metamorphosis (15 mm SL) (Figure 7).

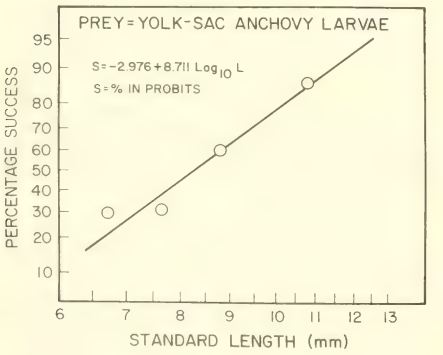


FIGURE 6.—Percentage of Pacific mackerel larvae (probit scale) that captured one or more yolk-sac anchovy larvae in relation to standard length of the mackerel (log_{10} scale). The length class was variable. Larvae were ranked by length and classes set at 10 observation intervals. The LD_{50} was 8.1 mm (95% confidence interval 7.2-9.5 mm).

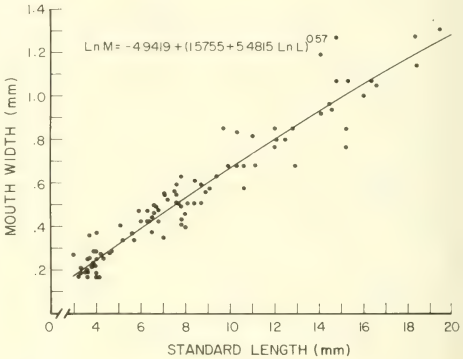


FIGURE 7.—Mouth width as a function of standard length of Pacific mackerel larvae. Points represent single larva.

The threshold, in terms of length for feeding on *A. salina* nauplii, was distinctly different from that for feeding on anchovy eggs. The 50% threshold for nauplii was 4.5 mm SL (95% confidence interval, 4.1-4.8 mm) and that for eggs was 12.2 mm SL (11.3-13.1 mm). This could be expected because anchovy eggs are nearly three times as large as *A. salina* nauplii. On the other hand, when feeding success was expressed as a function of the ratio, mean prey width/mean mouth width, the percentage feeding success of Pacific mackerel fed *A. salina* was similar to that of larvae fed eggs (Figure 8). At first feeding, relative prey size (prey width/mouth width) was near unity for larvae fed either *A. salina* or eggs, indicating the width of the mouth established the upper size limit of prey. Since the 50% threshold for relative prey size for the combined data given in Figure 8 was 0.85 (95% confidence interval,

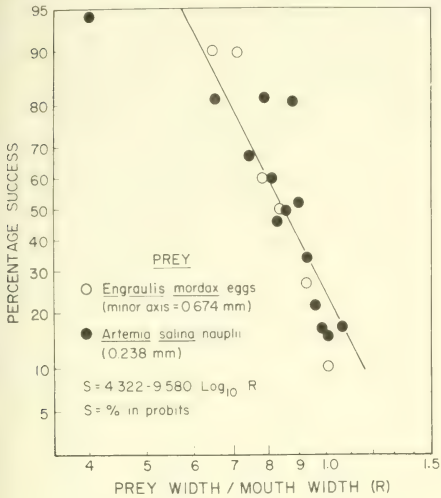


FIGURE 8.—Relation between average feeding success (probit scale) and average relative prey size (prey width/mouth width), for larval groups fed *Artemia salina* nauplii (closed circles) and northern anchovy eggs (open circles). Each point is the percentage success of fish within a mouth width/prey size class, where $n>9$. Line is the regression of percentage success probit on $\log_{10}$ of the prey-width to mouth-width ratio, for *A. salina* nauplii and anchovy egg data combined. The LD_{50} for the combined data was 0.85 (95% confidence interval 0.79-0.91).

0.79-0.91) and the 95% threshhold was 0.57 (0.47-0.70), nearly all Pacific mackerel larvae (95%) were able to ingest a prey when it was 57% of the width of the mouth and 50% were able to do so when it was 85% of the mouth width.

Nearly all prey eaten by Pacific mackerel larvae in the sea fell within the range of sizes predicted from the laboratory work; few prey exceeded the width of the mouth (Figure 9). Fifty-nine percent of all identifiable food items in the stomachs of sea-caught larvae were stages of copepods; other items included cladocerans, oikopleurans, gastropods, invertebrate eggs, diatoms, fecal pellets, and one fish larvae.

Although laboratory data indicated that 50% of Pacific mackerel larvae were able to ingest prey having a width of 85% of the mouth width, the mean diameter of prey eaten in the sea was 38±2% (2 SE) of the mouth width. Thus, a substantial number of prey eaten by larvae in the sea was much smaller than the maximum size of prey they were capable of ingesting. This may reflect a shortage of larger prey in the sea. Larger prey probably are important nutritionally. If one assumes the prey given in Figure 8 to be spherical, then 50% of the prey items accounted for about 85-90% of the total volume of food, depending on larval size. Conversely, the small prey items that contributed 50% by number, contributed only 10-15% of the total volume of prey eaten. This calculation underestimates the volume of the larger prey because they are more elongate or less spherical than smaller ones. Nevertheless, it indicates that prey less than the mean size eaten contributed relatively little nutritionally to the diet of Pacific mackerel larvae, and that the relatively large, but more rare, prey probably made the major contribution to growth.

Ration, Growth Efficiency and Metabolism

Pacific mackerel larvae (age 3-5 d) fed actively throughout the day; the gut was filled within the first hour of feeding and it remained full throughout the remainder of the 12-h feeding day, despite a high rate of gastric evacuation. Evacuated *Brachionus plicatilis* were well digested; only the lorica remained after digestion. Our measurements of evacuation rates indicated that about half the gut contents was evacuated in 2 h (Figure 10). Growth of larvae used for ration estimates was about the same as that for other groups reared at 19° C (Figure 3). To grow at this rate in the laboratory, Pacific mackerel larvae (age 3-5 d) consumed an average of about 87% of their dry body weight per day, or about 165-538 rotifers/day (Table 3). This estimate of ration was based on the dry weight of the mean number of rotifers in stomachs, adjusted for the rate of evacuation (Stauffer 1973). The mean gross growth efficiency in dry weight was 33%, which falls within the range of estimates for fish larvae and young fishes (Pandian 1967; Stepien 1976).

Our respiration experiments indicated that Pacific mackerel larvae at 18.0° C consumed 6.1±1.4 (2 SE) μl O_2/mg per h (n = 24) and at 22.0° C they consumed 11.4±3.0 μl O_2/mg per h (n = 14). By interpolation, the rate at 19° C, the temperature of the ration experiments, is estimated as 7.4 μl O_2/mg per h. This metabolic expenditure, converted to calories per day (footnote 6, Table 3) was, on the average, about 18% of the mean daily ration for larvae given in the table. This is probably an underestimate of their metabolic requirement because the activity of larvae confined in

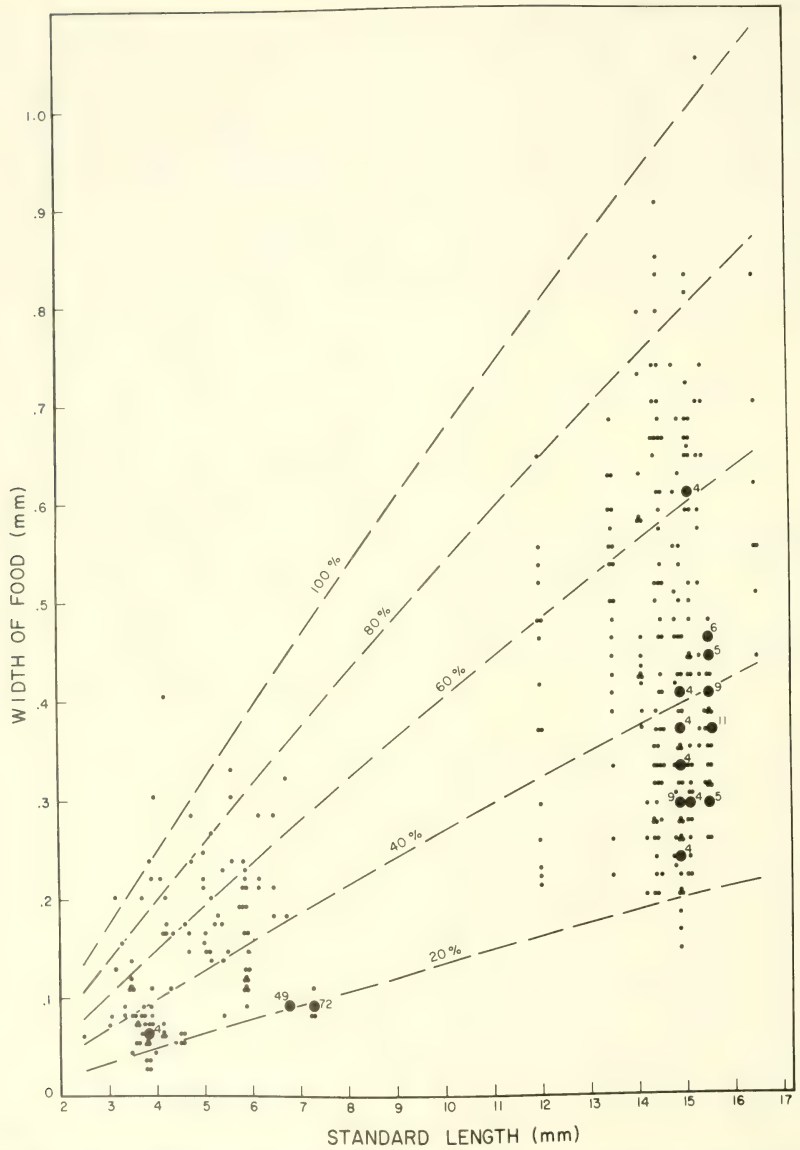


FIGURE 9.—Width of foods eaten in the sea by Pacific mackerel larvae of various standard lengths. Each small point is the width of a single prey; larger points represent multiple points for prey of the same size and number observations. Dashed lines indicate the prey width equal to 20-80% of the mouth width, or equal to the mouth width (100%), for Pacific mackerel larvae of 3-16 mm (calculated from data given in Figure 7).

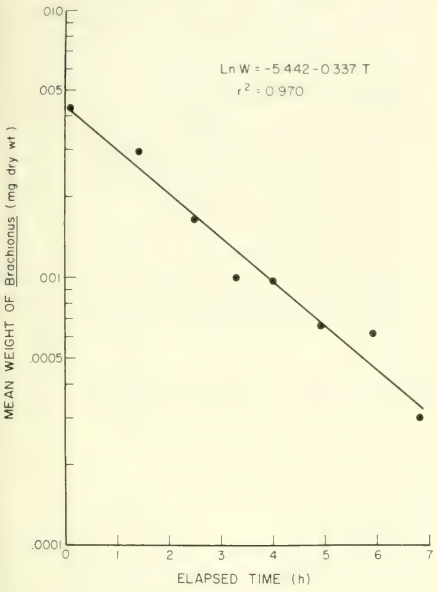


FIGURE 10.—Rate of gastric evacuation of 4.01±0.03 mm SL Pacific mackerel larvae fed *Brachionus plicatilis*. Each point represents the mean dry weight of *B. plicatilis* in guts of 13-16 larvae. Dry weight estimated by counting numbers of *B. plicatilis* in stomachs and multiplying by the mean dry weight of one *B. plicatilis* (0.16 μg) (Theilacker and McMaster 1971).

Warburg flasks was probably less than that of free-swimming larvae. These respiration measurements do establish a lower limit to food ration, because the ration would have to exceed the metabolic requirement just to meet maintenance costs.

DISCUSSION

The characteristics of the embryonic period (duration of incubation and yolk-sac periods, extent of yolk reserves, size at first feeding, and ability to withstand starvation) were similar to other temperate fishes with small pelagic eggs (Lasker et al. 1970; Zweifel and Lasker 1976) and did not differ greatly from some subtropical species (Houde 1974). Small differences in these characteristics may be of importance (Houde 1974) but growth, metabolism, feeding, and swimming behavior are of more value in characterizing the early life history of Pacific mackerel.

Pacific mackerel larvae grew rapidly, completing metamorphosis (15 mm SL) in 2-3 wk. Fast growth appears to be characteristic of scombroid larvae and is even more rapid in tropical scombroids: *Auxis thazard* grew to 64 mm SL in 17 d (Harada, Murata, and Furutani 1973) and *A. tapeinosoma* grew to 49 mm SL in 18 d (Harada, Murata, and Miyashita 1973). Fast growth requires a large food ration; we found that Pacific mackerel larvae consumed about 87% of their dry

TABLE 3.—Estimate of ration, metabolism, and growth efficiency of 3-5 d old Pacific mackerel larvae fed *Brachionus plicatilis*.

Larval age (d)	Experimental conditions: Temperature (°C)	Larval SL±2 SE (mm)	Larval weight[1]: On day of ration estimation (μg)	Larval weight[1]: Gain 1 d after estimation (μg)	Food density (no./ml)	Mean weight in stomachs[2]: No. of samples[3]	Mean weight in stomachs[2]: $\bar{x}$ ±2 SE (μg)
3	18.7	3.66±0.03	37.8	5.2	157	7	4.8±0.8
4	19.0	3.76±0.02	43.0	14.0	47	8	6.9±1.0
5	19.4	4.38±0.08	84.6	37.5	198	7	15.6±4.5
$\bar{x}$	19.0	3.93	55.1	18.9	134		9.1

Larval age (d)	Ration, metabolism, and growth efficiencies: Ration[4] μg·d	Ration[4] Percent body weight·d	Ration[4] [5]cal·d	Metabolic rate[6] (cal/d)	Weight gain[7] (cal)	Gross growth efficiency[8] (percentage)
3	26.5	70	0.141	0.0338	0.026	20
4	38.1	89	0.203	0.0384	0.070	37
5	86.2	102	0.460	0.0756	0.188	44
$\bar{x}$	50.3	87	0.268	0.0493	0.094	33

[1]Calculated from mean larval length using relation given in Figure 4.
[2]Mean counts of *B. plicatilis* in stomach converted to weight using one *B. plicatilis* = 0.16 μg (Theilacker and McMaster 1971).
[3]Each sample consisted of 13-16 larvae; sampling began after first hour of feeding.
[4]Ration = $(r \cdot k \cdot t) \div r$, where r is mean stomach contents, k is rate of gastric evacuation (0.377), and t is duration of feeding period (12 h). (From G. Stauffer, unpubl. manuscr., Southwest Fisheries Center, La Jolla, Calif.)
[5]Caloric value of *B. plicatilis* = 5,335 cal/g (Theilacker and McMaster 1971).
[6]Maintenance requirement from: 7.45 μl O_2/mg per h; 1 μl O_2 = 0.005 cal; time = 24 h; and dry weight of larvae on day ration estimated.
[7]Caloric value of weight gained assumed to equal 5,000 cal/g.
[8]Gross efficiency (dry weight) = weight gain/ration.

weight per day and weight increased from 0.034 mg to 7.5 mg over the larval period. To capture sufficient numbers of prey to support such rapid growth requires that the size of the prey and the size of the mouth increase rapidly. Our analysis of sea-caught Pacific mackerel larvae showed that the maximum size of prey did increase rapidly, more or less, in proportion to mouth size. The mean and minimum size of prey eaten by Pacific mackerel changed more slowly but the smaller prey, those less than the average size, may constitute <15% of the volume of food eaten. A similar pattern of rapidly increasing prey size with length also has been documented for *Scomber japonicus* larvae by Shirota (1970) and Yokota et al. (1961).

A dependency on larger prey and fast growth requires faster swimming to increase the volume of water searched for prey because abundance declines with increased prey size (Sheldon et al. 1972). The swimming behavior of Pacific mackerel larvae appeared consistent with this argument. Cruising speeds increased rapidly with length, roughly to the 1.8 power, and speeds of the larger larvae were at the upper end of the range, typical of larval fishes (3 SL/s) (Blaxter 1969). Higher speeds require a greater metabolic expenditure. The rate of oxygen consumption for Pacific mackerel (6-11 μl O_2/mg per h) was above that for other marine fish larvae (Blaxter 1969) indicating a higher-than-average metabolic expenditure despite the fact that the rates probably do not reflect the entire cost of high speed swimming.

Piscivorous feeding was an important behavioral trait in the early life history of Pacific mackerel because larvae were no longer limited to prey sizes equal to or less than the size of an open mouth. In piscivorous feeding, prey were seized, manipulated and the mouth greatly expanded during ingestion, permitting consumption of much larger diameter foods. In our samples of sea-caught larvae, only one stomach contained a larval fish, but the actual incidence may be higher because larvae are digested rapidly. Cannibalism, a correlate of piscivorous feeding, was common in laboratory groups after the larvae reached 8 mm SL. This also has been observed from stomach contents of the Atlantic mackerel, *S. scombrus* (Lett 1978). Cannibalism appears to be a common feature of scombroid life history; Mayo (1973) remarked that *Euthynnus alletteratus*, *Scomberomorus cavalla*, *S. regalis*, and *Auxis* sp. became cannibalistic at about 5 mm SL. He also noted that cannibalism ceased as the fish became juveniles which agrees with our observation that cannibalism ended as Pacific mackerel approached metamorphosis and began to school. The extent that cannibalism affected the form of our laboratory growth curves is unknown. Although cannibalism was high in all groups, survival was higher in groups reared at high temperatures because of the faster growth rate, which meant faster transit through cannibalistic sizes.

In summary, traits that characterize the early life history of Pacific mackerel are the interrelated characteristics of fast growth, fast swimming, high metabolism, a dependence on increasingly larger prey, and cannibalism. The high food requirements of the larvae, and the fact that in the sea they feed upon many prey substantially smaller than they are capable of eating, indicates that growth or survival in the sea might be limited by the availability of larger prey.

LITERATURE CITED

ARTHUR, D. K.
1976. Food and feeding of larvae of three fishes occurring in the California Current, *Sardinops sagax*, *Engraulis mordax*, and *Trachurus symmetricus*. Fish. Bull., U.S. 74:517-530.

BLAXTER, J. H. S.
1969. Development: eggs and larvae. *In* W. S. Hoar and D. J. Randall (editors), Fish physiology, Vol. 3, p. 177-252. Acad. Press, N.Y.

BLAXTER, J. H. S., AND G. HEMPEL.
1963. The influence of egg size on herring larvae. J. Cons. 28:211-240.

FINNEY, D. J.
1952. Probit analysis: a statistical treatment of the sigmoid response curve. Univ. Press, Camb., 318 p.

HARADA, T., O. MURATA, AND H. FURUTANI.
1973. On the artificial fertilization and rearing of larvae in Marusōda, *Auxis tapeinosoma*. [In Jpn., Engl. abstr.] J. Fac. Agric., Kinki Univ. 6:113-116.

HARADA, T., O. MURATA, AND S. MIYASHITA.
1973. On the artificial fertilization and rearing of larvae in Hirasōda, *Auxis thazard*. [In Jpn., Engl. abstr.] J. Fac. Agric., Kinki Univ. 6:109-112.

HOUDE, E. D.
1974. Effects of temperature and delayed feeding on growth and survival of larvae of three species of subtropical marine fishes. Mar. Biol. (Berl.) 26:271-285.

HUNTER, J. R.
1972. Swimming and feeding behavior of larval anchovy *Engraulis mordax*. Fish. Bull., U.S. 70:821-838.
1976. Culture and growth of northern anchovy, *Engraulis mordax*, larvae. Fish. Bull., U.S. 74:81-88.

HUNTER, J. R., AND J. R. ZWEIFEL.
1971. Swimming speed, tail beat frequency, tail beat amplitude, and size in jack mackerel, *Trachurus symmetricus*, and other fishes. Fish. Bull., U.S. 69:253-266.

KISLALIOGLU, M., AND R. N. GIBSON.
1976. Prey 'handling time' and its importance in food

selection by the 15-spined stickleback, *Spinachia spinachia* (L.) J. Exp. Mar. Biol. Ecol. 25:151-158.

KRAMER, D.
1960. Development of eggs and larvae of Pacific mackerel and distribution and abundance of larvae 1952-1956. U.S. Fish. Wildl. Serv., Fish. Bull. 60:393-438.

KRAMER, D., AND P. E. SMITH.
1970. Seasonal and geographic characteristics of fishery resources, California Current region—IV. Pacific mackeral. Commer. Fish. Rev. 32(10):47-49.

LASKER, R.
1964. An experimental study of the effect of temperature on the incubation time, development, and growth of Pacific sardine embryos and larvae. Copeia 1964:399-405.

LASKER, R., H. M. FEDER, G. H. THEILACKER, AND R. C. MAY.
1970. Feeding, growth, and survival of *Engraulis mordax* larvae reared in the laboratory. Mar. Biol. (Berl.) 5:345-353.

LEONG, R.
1977. Maturation and induced spawning of captive Pacific mackerel, *Scomber japonicus*. Fish. Bull., U.S. 75:205-211.

LETT, P. F.
1978. A comparative study of the recruitment mechanisms of cod and mackerel, their interaction and its implication for dual stock management. Ph.D. Thesis, Dalhousie Univ., Halifax, 125 p.

MAYO, C. A.
1973. Rearing, growth, and development of the eggs and larvae of seven scombrid fishes from the Straits of Florida. Ph.D. Thesis, Univ. Miami, 127 p.

PANDIAN, T. J.
1967. Intake, digestion, absorption, and conversion of food in the fishes *Megalops cyprinoides* and *Ophiocephalus striatus*. Mar. Biol. (Berl.) 1:16-32.

SHELDON, R. W., A. PRAKASH, AND W. H. SUTCLIFFE, JR.
1972. The size distribution of particles in the ocean. Limnol. Oceanogr. 17:327-340.

SHIROTA, A.
1970. Studies on the mouth size of fish larvae. [In Jpn., Engl. summ.] Bull. Jpn. Soc. Sci. Fish. 36:353-368. (Transl. by Fish. Res. Board Can., Transl. Ser. 1978.)

STAUFFER, G.
1973. A growth model for salmonids reared in hatchery environments. Ph.D. Thesis, Univ. Washington, Seattle, 213 p.

STEPIEN, W. P., JR.
1976. Feeding of laboratory-reared larvae of the sea bream *Archosargus rhomboidalis* (Sparidae). Mar. Biol. (Berl.) 38:1-16.

THEILACKER, G. H., AND M. F. MCMASTER.
1971. Mass culture of the rotifer *Brachionus plicatilis* and its evaluation as a food for larval anchovies. Mar. Biol. (Berl.) 10:183-188.

UMBREIT, W. W., R. H. BURRIS, AND J. F. STAUFFER.
1964. Manometric techniques. A manual describing methods applicable to the study of tissue metabolism. Burgess, Minneap., 305 p.

WATANABE, T.
1970. Morphology and ecology of early stages of life in Japanese common mackerel, *Scomber japonicus* Houttuyn, with special reference to fluctuation of population. [In Jpn., Engl. abstr.] Bull. Tokai Reg. Fish. Res. Lab. 62:1-283.

WEBB, P. W.
1975. Hydrodynamics and energetics of fish propulsion. Fish. Res. Board Can., Bull. 190, 158 p.

WOLFSON, F. H.
1965. The optical comparator as a tool in plankton research. Limnol. Oceanogr. 10:156-157.

YOKOTA, T., M. TORIYAMA, F. KANAI, AND S. NOMURA.
1961. Studies on the feeding habit of fishes. [In Jpn., Engl. summ.] Rep. Nankai Reg. Fish. Res. Lab. 14, 234 p.

ZWEIFEL, J. R., AND R. LASKER.
1976. Prehatch and posthatch growth of fishes—a general model. Fish. Bull., U.S. 74:609-621.

SPAWNING AND FECUNDITY OF ATLANTIC MACKEREL, *SCOMBER SCOMBRUS*, IN THE MIDDLE ATLANTIC BIGHT

WALLACE W. MORSE[1]

ABSTRACT

Collections of Atlantic mackerel, *Scomber scombrus*, were made during spring 1977 from Maryland to Rhode Island. Length-weight relationships were determined for total and fork lengths and total and gutted weights. Spawning time was determined from gonad somatic indices and peak spawning occurred between 21 April and 4 May. Egg diameter frequencies from running ripe ovaries indicated five to seven egg batches are spawned by each female during the spawning season. Fecundity was estimated and ranged from 285,000 to 1,980,000 for fish between 307 and 438 mm fork length. Fecundity was related to fork length, gutted weight, and age.

The Atlantic mackerel, *Scomber scombrus* Linnaeus, is a schooling, pelagic species ranging from the Gulf of St. Lawrence to North Carolina in the northwest Atlantic and from Norway to Spain in the northeast Atlantic. The northwest Atlantic population has been separated into northern and southern contingents on the basis of size composition, spawning times, summer distributions, and tagging studies (Sette 1950; Moores et al. 1975; MacKay[2]).The northern contingent spawns in the southern Gulf of St. Lawrence from about the end of May to mid-August (Ware 1977). The southern contingent spawns from mid-April to June from North Carolina to Massachusetts (Berrien 1978).

Fecundity estimates of northwest Atlantic mackerel are limited to a few observations ranging from about 500,000 to 1,000,000 eggs (Brice 1898: 208-213; Sette 1943). Fecundity of northeast Atlantic mackerel ranged from approximately 130,000 to 1,100,000 eggs for fish 28.5-46.0 cm total length (Macer[3]; Lockwood[4]). This paper presents the results of a fecundity and spawning time investigation of the southern contingent.

METHODS

Atlantic mackerel were collected between 9 April and 21 May 1977 from recreational and commercial catches from Maryland to Rhode Island (Table 1). Length frequencies of males and females are shown in Figure 1. All fish were measured to the nearest millimeter fork length (FL) and total length (TL), and weighed to the nearest gram total weight (TW) and gutted or somatic weight (GW). Otoliths were extracted for age determination. Ovaries of all mature females were exsected, weighed to the nearest 0.01 g, and preserved in 10% Formalin.[5]

Preliminary observations of eggs from ovaries in the spawning condition revealed that three egg types were present: 1) small, translucent eggs; 2)

[1]Northeast Fisheries Center Sandy Hook Laboratory, National Marine Fisheries Service, NOAA, Highlands, NJ 07732.

[2]MacKay, K. T. 1973. Aspects of the biology of Atlantic mackerel in ICNAF Subarea 4. Int. Comm. Northwest Atl. Fish., Res. Doc. 73/70, 11 p.

[3]Macer, C. T. 1976. Observations on the maturity and fecundity of mackerel (*Scomber scombrus* L.) Int. Counc. Explor. Sea, CM 1976/H:6, 7 p.

[4]Lockwood, S. J. 1978. The fecundity of mackerel, *Scomber scombrus* L. Int. Counc. Explor. Sea, CM 1978/H:9, 5 p.

[5]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Catch data of Atlantic mackerel sampled in 1977.

Date	Port	Numbers of fish examined		Capture method
		Female	Male	
9 April	Ocean City, Md.	16	8	Otter trawl
16	Cape May, N.J.	15	10	Hook and line
20	Ocean City	26	26	Otter Trawl
25	Barnegat, N.J.	20	25	Hook and line
27	Greenport, N.Y.	64	36	Pound net
28	Belford, N.J.	10	15	Otter trawl
28	Sheepshead Bay, N.Y.	6	16	Hook and line
30	Sheepshead Bay	9	12	Hook and line
1 May	Sheepshead Bay	6	17	Hook and line
4	Barnegat	16	36	Hook and line
5	Barnegat	39	66	Hook and line
7	Sheepshead Bay	11	19	Hook and line
8	Point Pleasant, N.J.	17	8	Hook and line
9	Point Judith, R.I.	42	43	Otter trawl
11	Belmar, N.J.	5	20	Hook and line
14	Sheepshead Bay	12	38	Hook and line
15	Sheepshead Bay	4	33	Hook and line
17	Sandy Hook, N.J.	22	20	Hook and line
18	Point Judith	32	48	Otter trawl
22	Sheepshead Bay	77	21	Hook and line
Totals		449	517	

Manuscript accepted August 1979.
FISHERY BULLETIN: VOL. 78, NO. 1, 1980.

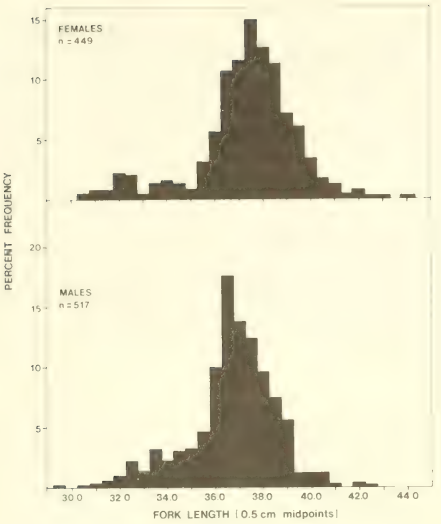


FIGURE 1.—Length frequencies of male and female Atlantic mackerel used in this study.

larger opaque, yolked eggs; and 3) large translucent eggs. There appeared to be no clear size separation between egg types, which is indicative of serial spawners (Hickling and Rutenberg 1936). Therefore, the method described by Hislop and Hall (1974) for whiting, *Merlangus merlangus*, was used to determine which eggs would be shed during the current spawning season. Since yolk deposition indicates eggs are ripening for spawning, random samples of 300 eggs were measured from ovaries at successive maturity stages to determine the average minimum size of yolked eggs. Eggs 0.20 mm and larger contained yolk and were included for fecundity estimation. Ovaries were classified into four maturity stages based upon macroscopic examination and the occurrence of mature eggs (Table 2). Egg diameter frequencies of yolked eggs from ovaries in the developing, ripe, running ripe, and partially spent condition are shown in Figure 2.

Ovaries in the ripe condition (Figure 2b) were used for fecundity estimations. If large translucent eggs (1.00-1.35 mm) were present in the lumen of the ovary, which is indicative of the running ripe condition (Figure 2c), the ovary was not utilized for fecundity because some eggs may have been shed and fecundity would be underestimated.

TABLE 2.—Maturity stages of Atlantic mackerel ovaries.

Stage	Description
1. Developing	Ovary enlarged, usually orange colored with a granular appearance. No translucent eggs, maximum egg diameters 0.8-0.9 mm.
2. Ripe	Ovary fills most of gut cavity, yellow colored, in advanced stage some translucent eggs are visible through wall. Maximum egg diameter 1.0-1.2 mm.
3. Running ripe	Similar in appearance to stage 2, eggs are extruded with pressure on abdomen of fish. Maximum egg diameters 1.2-1.4 mm.
4. Partially spent	Ovary is flaccid, often hemorrhaging is evident at anterior portion of ovary, some residual mature eggs (1.1-1.4 mm) present.

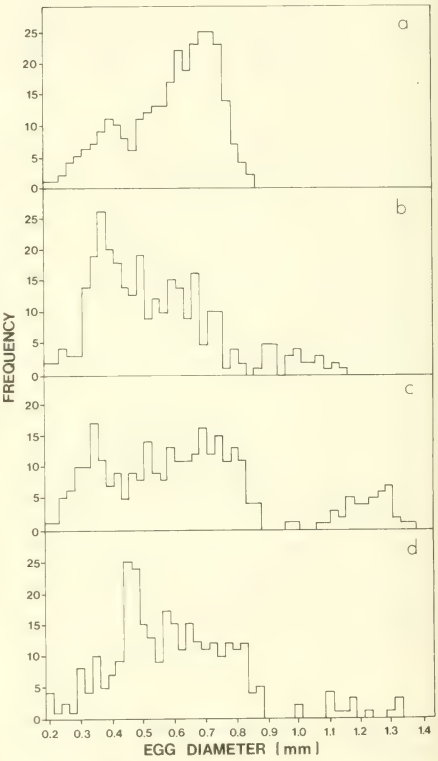


FIGURE 2.—Egg diameter frequencies of Atlantic mackerel ovaries in stages: developing (a), ripe (b), running ripe (c), and partially spent (d). Each graph based on 300 egg measurements.

Suitable ovaries were removed from the Formalin solution, placed in glacial acetic acid for 5 min, and washed, and the eggs were separated with a gentle

stream of water and agitated in a 0.20 mm mesh sieve. Following removal of the ovarian tissue, the eggs were air dried on blotter paper for 2-3 min and weighed (±0.01 g), and two subsamples were removed and weighed (±0.01 mg). All eggs in each subsample were counted and the mean used to calculate total egg numbers based on the weight of all eggs in the ovary. If the two subsample counts differed by 10% or more, additional samples were taken until two counts differed by <10%.

Ages were determined from otoliths as described by Steven (1952).

RESULTS

The allometric relationships of length-weight were expressed by the power function:

$$Y = aX^b \quad (1)$$

where X is length, Y is weight, and a and b are constants. Equation (1) was converted to the linear form by a logarithmic (base 10) transformation to:

$$\log Y = \log a + b \log X . \quad (2)$$

The interrelationships between length measurements and between weight measurements were expressed by the linear function:

$$Y = a + bX \quad (3)$$

where Y and X are both length or both weight. All data were fitted using least-squares regression techniques.

Predictive regression equations were calculated using all observations for males and females and an analysis of covariance applied to determine possible sex related differences. No significant differences ($P = 0.05$) were indicated between sexes and sexes were therefore pooled. The pooled regression equations and associated statistics are presented in Table 3.

To determine the peak spawning time the mean gonad somatic index (GSI = percent ovary weight of the gutted weight) was calculated for each week of the sampling period (Figure 3). It appears that individual fish attain their maximum GSI just prior to spawning the first egg batch and a decline in GSI occurs as successive batches are spawned. This was shown by comparing the mean GSI of each maturity stage (Table 4) which showed an increase from stage 1 to 3 and a rapid decrease at stage 4. Similar results were reported by Kaiser (1973) for horse mackerel, *Trachurus murphyi*. He found that gonad somatic indices reflected maturation changes of the ovaries and a sharp decline in the mean GSI coincided with the appearance of the earliest spawning females. In this study the weekly mean GSI increased during the first 3 wk of sampling, peaked between 21 April and 4 May, and then declined steadily through the end of the sampling (22 May). All females examined from the last sampling week were partially spent and indicated spawning was nearly completed within the study area.

TABLE 3.—Length and weight relationships of Atlantic mackerel collected in the Middle Atlantic Bight, 1977. TW = total weight (grams); GW = gutted weight (grams); TL = total length (millimeters); and FL = fork length (millimeters). Symbols refer to the equation $Y = a + bX$; n = sample size; r = correlation coefficient; $S_{y.x}$ = standard deviation about the line.

Y	a	b	X	n	r	$S_{y.x}$
Curvilinear relationships between transformed variates						
log TW	-5.767	3.275	log TL	966	0.905	0.036
log GW	-5.420	3.106	log TL	966	0.924	0.030
log TW	-5.780	3.334	log FL	966	0.905	0.036
log GW	-5.374	3.140	log FL	966	0.924	0.030
Linear relationships between untransformed variates						
TL	1.793	1.098	FL	966	0.986	3.594
TW	-20.410	1.282	GW	966	0.979	22.397

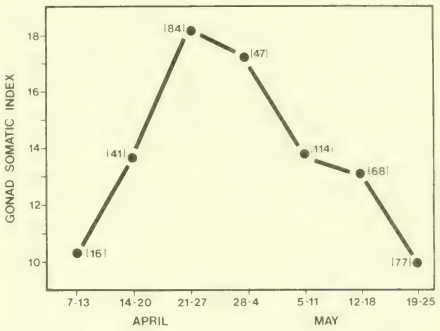


FIGURE 3.—Mean gonad somatic index (ovary weight as a percent of gutted weight) plotted by week for Atlantic mackerel sampled in 1977. Numbers in parentheses are sample sizes.

TABLE 4.—Mean gonad somatic index (GSI) and standard deviation for each maturity stage of Atlantic mackerel.

Stage	Mean GSI	SD	n
1. Developing	10.4	2.9	68
2. Ripe	15.0	4.2	247
3. Running ripe	24.9	4.7	41
4. Partially spent	8.6	2.2	93

The egg diameter frequencies shown in Figure 2 indicate Atlantic mackerel are serial spawners, i.e., several batches of eggs are shed by individuals throughout the spawning season. The presence of multiple modes in the egg diameter frequencies (Figure 2a-c) and ripening eggs in partially spent ovaries (Figure 2d) are indicators of serial spawning (Clark 1935; MacGregor 1957). A cytological study by Bara (1960) has shown that eggs are not shed continuously as stated by Cunningham (1889) but are shed in several batches during the 2-mo spawning period.

The potential number of batches spawned was estimated by determining the ratio of ripe eggs to all yolked eggs in six running ripe ovaries. Atlantic mackerel eggs, from plankton samples, ranged from 1.01 to 1.29 mm diameter (Berrien 1975; Ware 1977); therefore, in this study, eggs 1.05 mm and larger were assumed to constitute the next egg batch to be spawned. The ratios ranged from 13.7 to 21.7% and averaged 17.0%. Thus the potential number of batches spawned per individual was five to seven and averaged six batches.

Fecundity estimates ranged from 285,000 to 1,980,000 eggs for fish between 307 and 438 mm FL. Preliminary plots indicated a curvilinear relationship existed for fecundity-length and a linear relationship for fecundity-weight and fecundity-age. However, correlation coefficients (r) were higher for the logarithmic relationships of fecundity-weight and fecundity-age, therefore, all variables were transformed and linear regression equations of the form $\log Y = a + b(\log X)$ were calculated. Data plots and the equations relating fecundity to fork length, gutted weight, and age are shown in Figures 4-6.

DISCUSSION

Spawning by the southern contingent of Atlantic mackerel apparently peaked during the 2-wk period between 21 April and 4 May 1977. This 2-wk period represents the mean peak spawning time within the study area (Maryland to Rhode Island) since there is a north and eastward progression of spawning during the spring migration (Bigelow and Schroeder 1953; Berrien 1978). Berrien et al.[6] observed the north and east progression

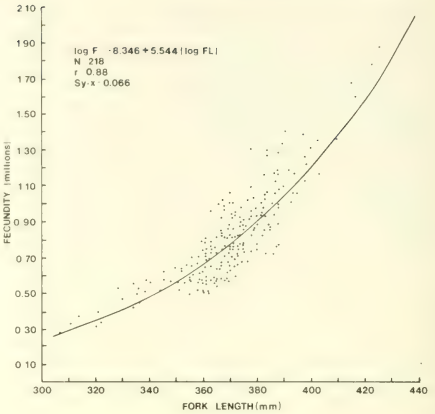


FIGURE 4.—Relationship of fecundity and length and the predictive logarithmic (base 10) regression for Atlantic mackerel in 1977.

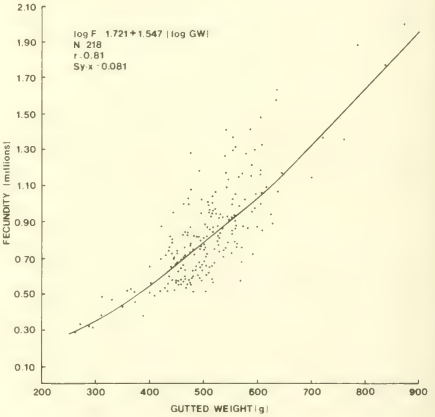


FIGURE 5.—Relationship of fecundity and weight and the predictive logarithmic (base 10) regression for Atlantic mackerel in 1977.

in plankton mackerel egg densities. They found spawning intensity in the Middle Atlantic Bight was low during mid-April and increased rapidly by late April, and maximum egg densities occurred about 25 April. Spawning continued at a reduced rate throughout May and then decreased steadily during June. Very similar results are indicated from my analysis of gonad somatic indices during the 1977 spawning season.

[6]Berrien, P. L., A. Naplin, and M. R. Pennington. 1979. Atlantic mackerel, *Scomber scombrus*, egg production and spawning population estimates for 1977 in the Gulf of Maine, Georges Bank, and Middle Atlantic Bight. Int. Counc. Explor. Sea ICES/ELH Symp./DS:9, 17 p.

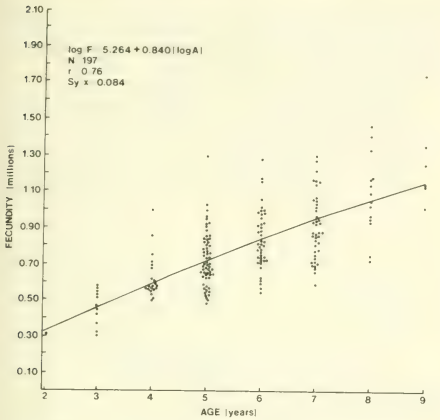


FIGURE 6.—Relationship of fecundity and age and the predictive logarithmic (base 10) regression for Atlantic mackerel in 1977.

Observations of spawning times of various temperate-water fish have indicated peak spawning dates may be relatively fixed. Cushing (1969) postulated an indirect link between the fixity of spawning season and the primary production cycle. Ware (1977) investigated the relationship of spawning time of Atlantic mackerel at St. Georges Bay, Nova Scotia, to the size and abundance of 80 μm plankton. He found the mean peak egg production date was 1 July $\pm$ 1 wk and coincided with the maximum abundance of summer plankton. It would appear, at least for the southern contingent, that the time of peak spawning is more variable than that indicated for St. Georges Bay. Sette (1943) determined maximum spawning occurred during mid-May (1928-32) off Middle Atlantic and southern New England States. Ichthyoplankton surveys during the mackerel spawning season in 1966 and 1975-77 (Berrien 1978; Berrien et al. see footnote 6; Berrien and Anderson[7]) within the Middle Atlantic Bight indicated spawning peaked during May in 1966 and 1975 and during April in 1976 and 1977. In fact, eggs were collected as early as 13 April in 1977. Berrien and Anderson (see footnote 7) attribute the April 1976 spawning peak to increased water temperatures within the study area.

The factors controlling the spawning time of Atlantic mackerel are unclear. The regularity shown by Ware (1977) would indicate internal control or a constant external stimulus such as photoperiod. Sette (1943) presented evidence indicating water temperature is a limiting factor controlling migration and in turn the timing of spawning in a fixed location. Cushing (1967, 1969) suggested that some fish spawn at a relatively fixed date that is linked to planktonic productivity and that changes in plankton production would cause dramatic changes in year-class success. It appears that a variable spawning date, as shown by the southern contingent—linked to the factors affecting plankton productivity, e.g., temperature, photoperiod, nutrient content—would increase the chances for larval survival.

The fecundity estimates presented here must be considered as maximum potential egg production because, as reported by Macer (see footnote 3), resorption may significantly reduce the number of eggs spawned. Preliminary observations by Macer indicated an average of 11.4% of yolked eggs were being resorbed. Bara (1960) observed degeneration in a "few" mature eggs though no quantitative data were presented. Studies are needed to define the extent and possible annual changes of resorption rates and their relationship to fecundity.

ACKNOWLEDGMENTS

I wish to thank Darryl Christensen and others who provided samples from the recreational catches throughout the course of this study. I appreciate the critical reviews and comments by E. Anderson and S. J. Wilk. Special thanks to M. Montone for typing this manuscript and M. Cox for preparation of the figures.

LITERATURE CITED

BARA, G.
1960. Histological and cytological changes in the ovaries of the mackerel, *Scomber scombrus* L., during the annual cycle. Rev. Fac. Sci. Univ. Istanbul, Ser. B, 25:49-86.

BERRIEN, P. L.
1975. A description of Atlantic mackerel, *Scomber scombrus*, eggs and early larvae. Fish. Bull., U.S. 73:186-192.
1978. Eggs and larvae of *Scomber scombrus* and *Scomber japonicus* in continental shelf waters between Massachusetts and Florida. Fish. Bull., U.S. 76:95-115.

[7]Berrien, P. L., and E. D. Anderson. 1976. *Scomber scombrus* spawning stock estimates in ICNAF Subarea 5 and Statistical Area 6, based on egg catches during 1966, 1975, and 1976. Int. Comm. Northwest Atl. Fish., Res. Doc. 76/XII/140, 10 p.

BIGELOW, H. B., AND W. C. SCHROEDER.
1953. Fishes of the Gulf of Maine. U.S. Fish Wildl. Serv., Fish. Bull. 53, 577 p.

BRICE, J. J.
1898. A manual of fish-culture, based on the methods of the United States Commission of Fish and Fisheries. Rep. U.S. Comm. Fish Fish. 23:1-261.

CLARK, F. N.
1935. Maturity of the California sardine (*Sardina caerulea*), determined by ova diameter measurements. Calif. Dep. Fish Game, Fish Bull. 42:5-49.

CUNNINGHAM, J. T.
1889. Studies of the reproduction and development of teleostean fishes occurring in the neighborhood of Plymouth. J. Mar. Biol. Assoc. U.K. 1:10-54.

CUSHING, D. H.
1967. The grouping of herring populations. J. Mar. Biol. Assoc. U.K. 47:193-208.
1969. The regularity of the spawning season of some fishes. J. Cons. 33:81-92.

HICKLING, C. F., AND E. RUTENBERG.
1936. The ovary as an indicator of the spawning period in fishes. J. Mar. Biol. Assoc. U.K. 21:311-316.

HISLOP, J. R. G., AND W. B. HALL.
1974. The fecundity of whiting, *Merlangus merlangus* (L.), in the North Sea, the Minch and at Iceland. J. Cons. 36:42-49.

KAISER, C. E.
1973. Gonadal maturation and fecundity of horse mackerel *Trachurus murphyi* (Nichols) off the coast of Chile. Trans. Am. Fish. Soc. 102:101-108.

MACGREGOR, J. S.
1957. Fecundity of the Pacific sardine (*Sardinops caerulea*). U.S. Fish Wildl. Serv., Fish. Bull. 57:427-449.

MOORES, J. A., G. H. WINTERS, AND L. S. PARSONS.
1975. Migrations and biological characteristics of Atlantic mackerel (*Scomber scombrus*) occurring in Newfoundland waters. J. Fish. Res. Board Can. 32:1347-1357.

SETTE, O. E.
1943. Biology of the Atlantic mackerel (*Scomber scombrus*) of North America. Part I: Early life history, including growth, drift, and mortality of the egg and larval populations. U.S. Fish Wildl. Serv., Fish. Bull. 50:149-237.
1950. Biology of the Atlantic mackerel (*Scomber scombrus*) of North America. Part II: Migrations and habits. U.S. Fish Wildl. Serv., Fish. Bull. 51:251-358.

STEVEN, G. A.
1952. Contributions to the biology of the mackerel, *Scomber scombrus* L. III. Age and growth. J. Mar. Biol. Assoc. U.K. 30:549-568.

WARE, D. M.
1977. Spawning time and egg size of Atlantic mackerel, *Scomber scombrus*, in relation to the plankton. J. Fish. Res. Board Can. 34:2308-2315.

RESPIRATION AND DEPTH CONTROL AS POSSIBLE REASONS FOR SWIMMING OF NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, YOLK-SAC LARVAE

DANIEL WEIHS[1]

ABSTRACT

Larval northern anchovy in the yolk-sac (nonfeeding) stage exhibit regular bursts of continuous swimming during the first 3 days after hatching. It has been suggested that this behavior may have a respiratory function. A different possibility is depth control, countering the tendency of the larvae to sink when motionless. This paper includes a theoretical and experimental investigation of the possible functions of these swimming bouts.

The theoretical approach was to define a model and calculate the oxygen available to the larva when resting and while moving, and experiments were performed as a check of the theoretical results. The experiments were conducted on yolk-sac larvae in sealed tanks with varying dissolved oxygen concentrations to determine the effects of reducing the available oxygen on the frequency and duration of the swimming bursts. Results of the experiments confirmed the theoretical model. They indicate that the swimming bouts both help the larva stay at a constant depth and have a respiratory function when the oxygen concentration in seawater is less than 60% of saturation.

Newly hatched northern anchovy, *Engraulis mordax*, larvae exhibit a pattern of regular short bouts of continuous swimming interspersed with periods of resting. These larvae are still in the yolk-sac stage and are not feeding so that the locomotory behavior must have some other purpose, as these motions are energy consuming and also endanger the animal by attracting predators (Lillelund and Lasker 1971). Hunter (1972) suggested that these swimming bouts might have a respiratory function. Respiration has to be by cutaneous diffusion through the 2-3 μm thick skin (Lillelund and Lasker 1971) of the larvae as the gills develop only at a later stage. The purpose of this paper is to test this hypothesis and another possibility, depth control, to counter sinking due to the negative buoyancy, using theoretical and experimental methods.

First, I develop a theoretical model for oxygen transport to motionless and swimming yolk-sac larvae and estimate the possible oxygen uptake. Next, I describe the experiments to test the prediction of the theory for both proposed mechanisms and compare their results.

[1]Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, Calif.; present address: Department of Aeronautical Engineering, Technion, Haifa, Israel.

Manuscript accepted: July 1979.
FISHERY BULLETIN: VOL. 78, NO. 1, 1980.

METHODS

Analytical Model

A mathematical model is now introduced to consider the possible respiratory function of the bouts of continuous swimming of yolk-sac anchovy larvae. First, we calculate the oxygen transport to a motionless larva. This transport is then compared with the metabolic requirements. If the metabolic requirements are not met, larval motion (and the resulting convective diffusion) is required.

The size of yolk-sac larvae (2.7-4.0 mm total length) and their swimming speeds (Hunter 1972) lead to typical Reynolds numbers, based on larval length (Weihs 1980) of <20. (The Reynolds number is a nondimensional factor indicating the relative importance of pressure and viscous effects on a body moving in a fluid under given circumstances—the higher the Reynolds number, the smaller the influence of the viscosity.) The larvae, as a direct result of their small size, are in a highly viscous laminar flow situation in which turbulent effects can be neglected. Thus, the larvae and their immediately surrounding water would be transported together in oceanic turbulent eddies, which are of the order of tens of centimeters in diameter. As a result, a nonswimming larva would stay for a relatively long period in the same mass

of water, even though that mass is convected on a much larger scale.

The motionless larva and its surrounding water mass may therefore be analyzed separately, as a distinct system in the thermodynamic sense. Within this system, oxygen transport to the larva is controlled by molecular diffusion because the gill system is not developed at this stage. This process is time dependent, beginning when the larva arrives in a certain location (by swimming) and rests, ending when swimming begins again. Initially the oxygen concentration in the water mass surrounding the larva is uniform, but the larva now starts acting as an oxygen sink, gradually depleting the oxygen content of the water surrounding it. This concept of the larva as an oxygen sink simplifies the calculations, as knowledge of the exact distribution of oxygen diffusivity on the animal's surface is not required. The sink model also is useful here as it averages out the direction of local transport and the body of the larva into which the oxygen diffuses can be taken as an equivalent sphere of equal surface area (Figure 1).

Diffusion into a sphere is most conveniently analyzed in the spherical coordinate system. The governing conservation of mass equation can be written (Crank 1975) as

$$\frac{\partial c}{\partial t} = D\left(\frac{\partial^2 c}{\partial r^2} + \frac{2}{r}\frac{\partial c}{\partial r}\right) \tag{1}$$

where c is the mass fraction of oxygen (a function of the distance and time); r is the radial distance, measured for the center of the equivalent spherical body (the sink); t is the time; and D is the diffusion coefficient of oxygen in seawater.

The temporal boundary condition is the initial, uniform state

$$c(r,0) = c_0 \tag{2}$$

while the spatial conditions are

$$c(\infty, t) = c_0 \tag{3}$$

which states that far from the animal the oxygen concentration stays unchanged at all times. Strictly, the condition should be defined at some finite distance but as that distance is much larger than the animal equivalent radius, it can be approximated by ∞. Next, the oxygen concentration boundary condition at the surface of the equivalent sphere $r = a$ is obtained. Muscles and vascularized tissues have much higher oxygen transport rates than seawater, due to internal uptake augmented by active transport. Thus, oxygen will be absorbed at the surface of the larva as fast as it arrives by diffusion from the surrounding water. The oxygen concentration c at the larva's surface ($r = a$) is thus constant, and very low, i.e.,

$$c(a,t) = c_1 \tag{4}$$

where $c_1 \to 0$ and $t > 0$.

Equations (2)-(4) enable solving equation (1) analytically, by classical methods. The solution can be written in nondimensional form for the concentration as

$$\frac{c - c_0}{c_1 - c_0} = \frac{a}{r}\,\mathrm{erfc}\,\frac{r-a}{2\sqrt{Dt}} \tag{5}$$

where the complementary error function, erfc, is defined as

$$\mathrm{erfc}(z) = \frac{2}{\sqrt{\pi}}\int_z^\infty e^{-z^2}\,dz\,. \tag{6}$$

Numerical values of the complementary error function are found in most mathematical tables (e.g., Abramowitz and Stegun 1965).

The rate of mass transfer (flux) J to the animal is now obtained from

$$J = -\rho D \int_A \frac{\partial c}{\partial r} dA \quad \text{(surface A)} \tag{7}$$

where ρ is the density and A the surface area of the body. For the equivalent sphere of radius a, $A = 4\pi a^2$. $\partial c/\partial r$ is assumed spherically symmetric so that

$$J = -\rho D A \left.\frac{\partial c}{\partial r}\right|_{r=a} \tag{8}$$

where the concentration derivative is obtained from Equation (5). Substituting this, and the value for the surface area, and setting $c_1 = 0$ as in Equation (4), the total mass flux per unit time J_d is

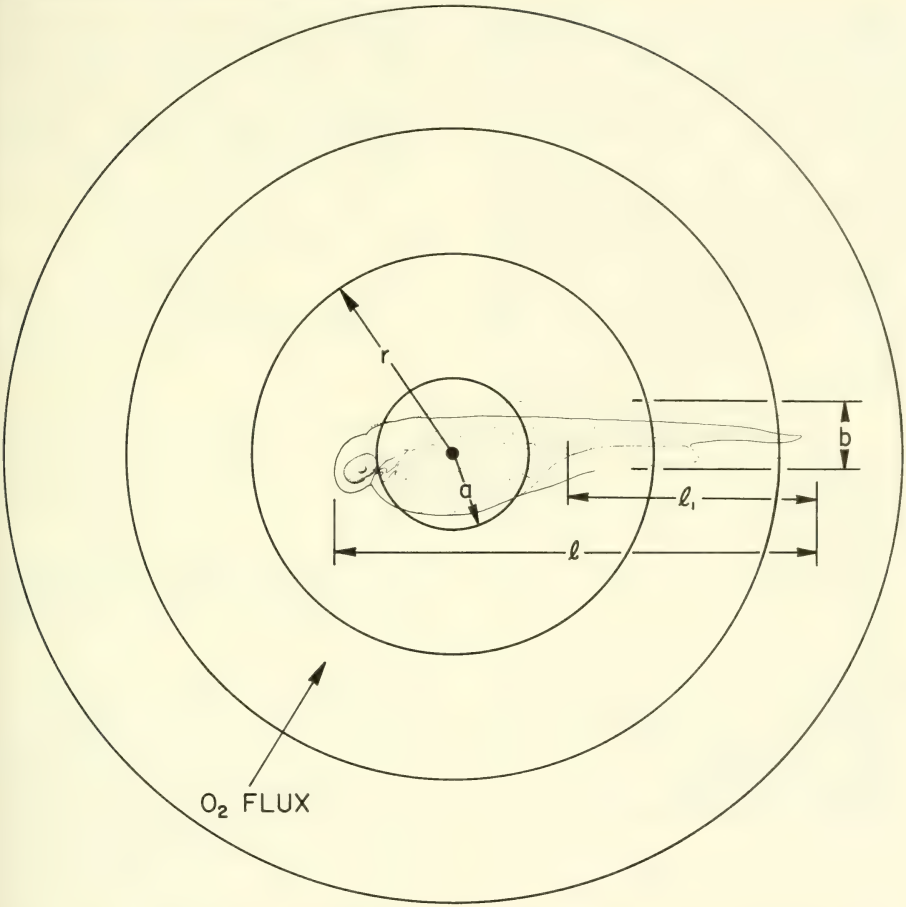


FIGURE 1.—Schematic description of model and spherical coordinate system centered on the center of mass of a northern anchovy larva: a is the radius of an equivalent sphere of equal surface area (not to scale), l is the larval length, and b and l_1 are the average tail strip depth and length.

$$J_d = -\rho D c_0 \cdot 4\pi r^2 \frac{a}{r} \operatorname{erfc}\left(\frac{r-a}{2\sqrt{Dt}}\right) \cdot \left(\frac{1}{2\sqrt{Dt}} + \frac{1}{r}\right) \qquad (9)$$

and when $r = a$, this simplifies to

$$J_d = 4\pi\rho D c_0 a^2 \left(\frac{1}{a} + \frac{1}{2\sqrt{Dt}}\right). \qquad (10)$$

Equation (10) consists of two terms in the brackets, multiplied by a constant factor. The first term in the brackets is the constant, time-independent contribution while the second describes the initial

transient. The latter drops rapidly, proportionally to the square root of time elapsed since arrival of the larva. Substituting numerical values into Equation (10), the oxygen flux can be compared with oxygen requirements of larval anchovy to see if the swimming motions are required for respiration.

The equivalent radius, a, of the larval anchovy is found by equating the surface area of the larva and the equivalent sphere. The larva, at this yolk-sac stage, is described for diffusion purposes as a sphere of radius q (the yolk sac) attached to an almost flat ribbon of length l_1 and average breadth b. The combined surface area of the sphere and ribbon is then taken to be equal to the area of the equivalent sphere appearing in Equation (10). Thus

$$4\pi a^2 = 2\, l_1\, b + 4\pi q^2. \qquad (11)$$

Using typical values for these parameters for newly hatched larvae we obtain $l_1 = 1.4$ mm, $b = 0.3$ mm, and $q = 0.3$ mm (from drawings by E. H. Ahlstrom, Senior Scientist, Southwest Fisheries Center, NMFS, NOAA, La Jolla, CA 92038), i.e., $a = 0.0395$ cm. The mass content of oxygen in seawater at 20° C is $c_0 = 7.8 \times 10^{-6}$ g/cm³ (Prosser 1973), and the mass fraction is obtained by dividing by the density of seawater, which then cancels out in Equation (10). Finally, the diffusion coefficient of oxygen is approximately equal for freshwater and seawater (Riley and Skirrow 1965) so that a reasonable value for 20° C is 1.8×10^{-5} cm²/s (O'Brien et al. 1978), or $D = 1.08 \times 10^{-3}$ cm²/min. Substituting all these values into Equation (10) we obtain

$$J = (4.18 + 2.51\, t^{-1/2})\, 10^{-9}\ \text{g/min} \qquad (12)$$

when the water is 100% saturated. Reducing the oxygen content of the water causes the value of the oxygen flux, J, to go down proportionally, i.e., by multiplying J from Equation (12) by the fraction of saturation. Some typical values of J appear in Figure 2 with the percent of saturation as the parameter.

When the larva starts swimming, two changes in the oxygen supply occur. First, the animal's motion produces a convective local flow relative to the body, thus bringing new, oxygen-rich water closer and removing the respiratory waste products. Secondly, the absolute motion will bring the larva to an area where the oxygen concentration is still at the initial ambient value, starting the process described by Equations (1)-(4) again.

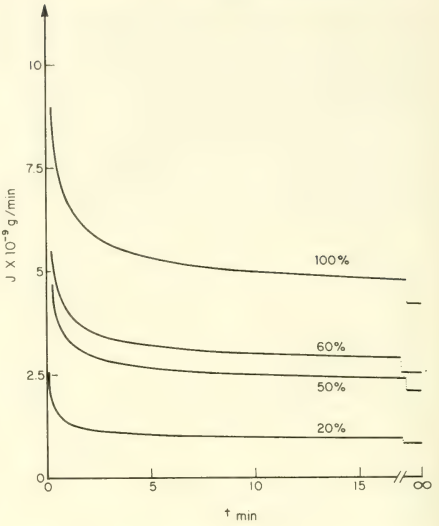


FIGURE 2.—Rate of oxygen transport (J) to motionless northern anchovy larva by diffusion versus time (t). Broken part of curve shows asymptotic value, after the initial transient has disappeared. Parameter is oxygen concentration in percentage of saturation.

Following this reasoning, even relatively slight motions causing just a local flow around the animal's body would suffice for respiratory functions. Thus, actual swimming would not be required. However, the yolk-sac larvae are increasingly negatively buoyant with age (Hunter and Sanchez 1976), which causes them to sink. Therefore, active absolute motion is necessary for the larva to stay at a given depth for feeding and future schooling.

When the larva is swimming, the process of transport of oxygen changes to convective diffusion, and as such is described by a different model (Daykin 1965). Daykin's work dealt with stationary eggs in a moving river environment, but for mass transfer purposes this is equivalent to a larva (or egg) moving at constant speed relative to the water. In the convective diffusion process (Levich 1962; Daykin 1965), the mass transfer to the larva can be roughly described by

$$J_{\text{con}} = 4\pi a^2 (c_0 - c_1) k \qquad (13)$$

where k is a diffusion coefficient obtained from experimental correlations of the diffusional flux with the Reynolds (Re) and Schmidt numbers (Sc). (The Schmidt number is the ratio of the kinematic viscosity to the diffusivity and nondimensionally indicates the relative importance of these two effects in a given flow situation.) For the present circumstances

$$k = \frac{D}{2a}(2 + 0.6\,\mathrm{Re}^{1/2}\,\mathrm{Sc}^{1/3}) \qquad (14)$$

for average swimming speeds of approximately 5 cm/s (Hunter 1972) and a Schmidt number of 600 we have

$$J_{con} = 1.27 \times 10^{-7}\ \text{g/min}. \qquad (15)$$

Hence, oxygen transport due to convective diffusion is over 20 times higher than for the motionless larva (Equation (12)). The calculation leading to Equation (15) is approximate, as the larva's shape will influence the coefficient 0.6 in k (Equation (14)) and also change the form of Equation (13). It is, however, accurate to at least an order of magnitude (Levich 1962). Thus, once the larva starts swimming, the mass transfer of oxygen to its surface increases by at least an order of magnitude. Recently, an additional mechanism for oxygen transport to stationary eggs was identified by O'Brien et al. (1978) who showed that under certain riverbed conditions natural convection, due to the oxygen and metabolite gradients, may contribute to the oxygen transfer. This effect may play a supplementary role in the present (pelagic) case as the natural convection effects are much smaller than the forced convection.

Tests with Larvae

Egg batches were obtained once a week from groups of adult northern anchovy maintained in the laboratory and induced to spawn. Measurements were made each week during a 6-wk period to minimize bias due to a single cohort group. Water temperature ranged from 19° to 21° C, and overhead fluorescent lighting was used. The 50% hatching point was determined and defined as "day 0" for each batch. Experiments were carried out on age day 0 larvae every week (six times).

A set of five 2,000 ml graduated cylinders filled with filtered seawater was used for the environmental tests. Oxygen concentrations of 100, 80, 60, 40, and 20% of saturation at the measured temperature were produced by bubbling nitrogen through each of the cylinders. After the larvae were added (about 25 individuals/cylinder), the cylinders were sealed off with rubber stoppers. Oxygen concentrations were measured periodically during the experiments with a Beckman Instrument Model 160 Physiological Gas Analyzer[2] to check on initial values and possible drift.

Individual fish were monitored for a 5-min period, and duration and number of swimming bursts were recorded on a Esterline-Angus Operation Recorder Model AW. Records were also made of approximate swimming direction (measured from horizontal) as well as the change in orientation of motionless larvae while they were sinking during the resting periods. Five active larvae were monitored in each container every week, for both day 0 and day 1 tests.

After the day 0 experiments were finished each week, the equipment was reset and the day 1 tests conducted 24 h later with additional larvae from the same batch. The latter larvae were kept in oxygen-saturated water from hatching to minimize stress due to oxygen starvation.

RESULTS

No appreciable change in the proportion of time spent in burst swimming was observed when the measurement at 100% of saturation concentration of oxygen (which is the oxygen level in the natural state in the sea because of turbulent interchange with the atmosphere) was compared with the time spent in motion at the 80 and 60% oxygen levels (Figure 3).

When oxygen levels were <60% of saturation, large increases in the time spent swimming were observed. The rate of increase of swimming time in both ages (day 0 and day 1) were similar. Various attempts at describing all five data points for each age-group by means of a single empirical exponential function were not successful (low coefficients of determination). Thus, it seems that a different behavioral mechanism is triggered when oxygen levels fall below 60% of saturation at the given temperatures, i.e., much lower than expected oxygen concentrations in the upper layers of the sea, where the anchovy larvae are usually found.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

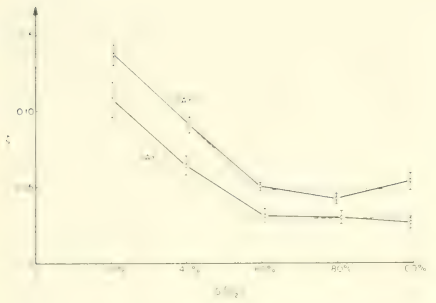


FIGURE 3.—Fraction of time spent actively swimming, ζ, versus oxygen concentration in percentage of saturation. $S[O_2]$, for newly hatched (day 0) and 24-h-old (day 1) northern anchovy larvae. Each point on the full curves is an average of between 20 and 25 individual 5-min observations. Bounds are standard errors. Dashed lines indicate idealized model of constant fraction, ζ, at high $S[O_2]$ and linearly increasing ζ at low $S[O_2]$.

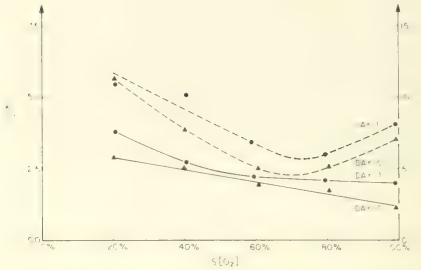


FIGURE 4.—Average duration (t) of swimming bouts (full lines) and number of bouts (n) in 5 min (dashed lines) for day 0 (solid triangles) and day 1 (solid circles) larvae, versus oxygen in percentage of saturation concentration ($S[O_2]$).

The duration of bursts increased monotonically as the oxygen levels decreased, while the number of bursts dropped significantly to a minimum of 1/min at 60-80%, increasing sharply after that (Figure 4). No satisfactory explanation has been found for the drop in the number of bursts at 80% of saturation. The main result illustrated by Figure 4 is that both the frequency and duration of bursts increase markedly at low oxygen concentrations, both contributing to the increase in time spent swimming.

The center of gravity of anchovy larvae is in the vicinity of the head and therefore they tend to be oriented in an oblique head-down configuration after swimming ceases. More mature larvae, which have converted significant amounts of yolk into denser tissue are negatively buoyant (Hunter and Sanchez 1976) and tend to sink head downward at rates of approximately 1-2 mm/s. To check the vertical station-keeping hypothesis, the direction of swimming was recorded, as well as the body orientation, when swimming started. The results of over 1,400 recorded swimming periods appear in Table 1, which lists average values of the body angle at the onset of swimming and the direction of swimming.

No significant variation in swimming direction with oxygen concentration was found for either day 0 or day 1 larvae (Table 1). The spread in results was large, as is noticeable from the standard errors. The total possible spread of data is $\pm 90°$, which suggests that swimming direction is actually a random phenomenon for day 0 larvae. At age 1 day, a positive bias was observed in the swimming direction, still with large variation. The body inclination at the beginning of the swimming periods was consistent, at around $-65°$ with the exception of the day 0, 20% oxygen data, which is influenced by additional factors, discussed below.

DISCUSSION

The analytical model predicted that a motionless larva would be able to pick up oxygen at a decreasing rate at any given spot (Equation 12).

TABLE 1.—Initial orientation of the body and duration of swimming during bouts of continuous swimming by newly hatched and 1-d-old northern anchovy larvae. Error bounds are standard error. Angles are measured from the horizontal. Positive values indicate upward motion. Averages of day 0 do not include 20% O_2 values as these (indicated by question marks) include different phenomena.

Oxygen concentration (% of saturation)	*N*, number of observed events		Orientation of body at start of swimming period (degrees)		Direction of swimming relative to horizontal (degrees)	
	Day 0 larvae	Day 1 larvae	Day 0 larvae	Day 1 larvae	Day 0 larvae	Day 1 larvae
100	106	157	−68.9±23.7	−74.6±11.8	−4.7±56.1	44.7±45.8
80	103	113	−66.3±29.4	−80.0± 9.2	−15.0±59.0	28.2±58.1
60	109	112	−72.1±15.6	−66.7±17.6	−3.9±73.6	51.9±31.9
40	161	140	−61.0±30.3	−69.2±22.0	12.3±54.0	33.2±45.9
20	210	204	−45.6±36.7(?)	−63.8±27.8	38.7±43.3(?)	37.4±52.3
Weighted average			−66.4±25.2	−70.2±16.9	−2.8±58.3	39.0±48.1

This prediction has now to be compared with the requirements of the organisms to determine if additional oxygen is needed. Data for oxygen consumption at 17° C of late-stage anchovy eggs and larvae of differing ages as a function of time since spawning has been obtained by Theilacker,[3] by measurement in a respirometer. These data were adjusted to 20° C, the temperature at which most of my experiments were conducted (Figure 5), by means of a temperature-growth correlation for larval northern anchovy (Zweifel and Hunter[4]). This adjustment was made by calculating the size of the larvae at 17° C at the ages recorded by Theilacker, then translating these into age for the same size at the new temperature, which gave a smaller size because growth rates increase with temperature. Thus, an estimate for the oxygen requirements at 20° C of size-defined larvae was obtained as a function of their age (the 20° C line in Figure 5).

The value of the ratio of oxygen consumption 1 d after hatching to that at hatching was about 1.6 (Figure 5). Returning now to Figure 3 we see that the ratio for the average percent of time spent swimming of the two age-groups is approximately 1.66. I conclude, therefore, that the distance between the day 0 and day 1 curves in Figure 3 is an indication of the increased general activity of the larvae as they grow. This correlation indicated in Figures 3 and 5 serves as an additional verification of both Theilacker's respirometer data and the present swimming data.

To compare experimental values of oxygen consumption to the prediction of the model we plot the data as Figure 6, where the horizontal lines show the range of oxygen requirements (from Theilacker's data) at hatching and 24 h later. The steady-state oxygen available by steady-state diffusion only (after the initial transient) obtained from the time-dependent first term in Equation (12) is now superimposed. Figure 6 indicates that pure diffusion supplies all the oxygen required for the day 0 larvae only when $<42\pm4\%$ of the O_2 saturation concentration is available. This changes to $63\pm4\%$ of saturation for the day 1 larvae. The sharp discontinuity in the swimming data, occurring be-

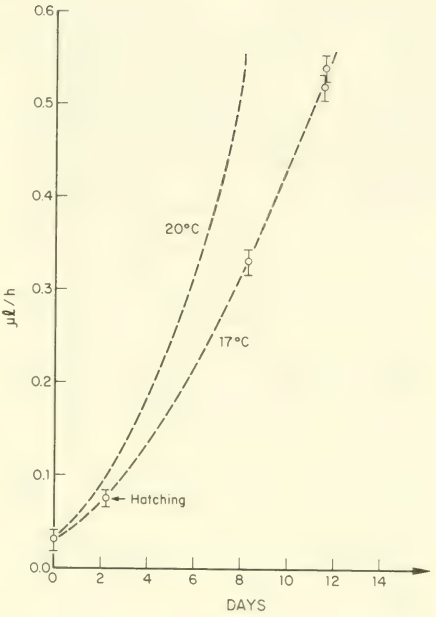


FIGURE 5.—Oxygen consumption by northern anchovy eggs and larvae versus time elapsed since spawning. Open circles indicate experimental data for 17° C. The line for 20° C is extrapolated from the 17° C data with the aid of the Zweifel and Hunter model (see text).

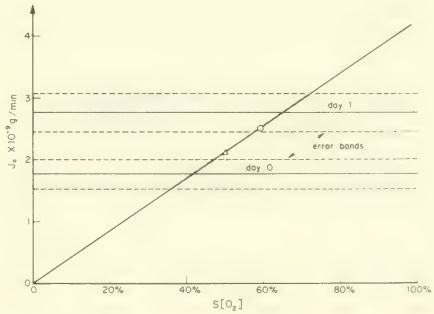


FIGURE 6.—Estimated oxygen requirements (J_0) of northern anchovy larvae at day 0 (hatching) and day 1, and steady-state oxygen supply by diffusion versus oxygen in percentage of saturation concentration (S[O_2]). The triangle and circle denote concentrations at which observed swimming behavior changes at day 0 and day 1, respectively (see Figure 3).

[3]G. Theilacker, Fishery Biologist, Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, CA 92030, pers. commun. November 1978.

[4]Zweifel, J. R., and J. R. Hunter. 1978. Temperature specific equations for growth and development of anchovy (*Engraulis mordax*) during embryonic and larval stages. Unpubl. manuscr., 37 p. Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, CA 92038.

tween 60 and 40% oxygen concentration (Figure 3) can now be understood in terms of the theoretical results above. When the oxygen concentration in this water is 60% or higher, diffusion alone can satisfy the respiratory requirements of both day 0 and day 1 motionless larvae. Thus, the swimming activity at the higher concentrations is due to other factors, such as depth control. The measured activity level (Figure 3) does not change between 60 and 100% oxygen concentration, as expected from the theoretical model's predictions.

The increased swimming activity observed when the concentration drops below the 40-60% level must therefore be a respiratory reaction. Active swimming causes convective diffusion (which, as shown in the Analytical Model section, leads to much higher oxygen transport rates) and moves the larva to a new, nondepleted position. As expected from this mechanism, activity increases with decreasing ambient oxygen concentration, as oxygen transport rates drop below the required level faster at low ambient concentration, initiating motion more often. The dashed lines in Figure 3 verify this theoretical reasoning and the obtained values of 59% concentration (day 1) and 55% concentration (day 0) for the beginning of respiration-driven swimming are in very good agreement with Figure 6, especially considering the experimental errors involved in the various data sources.

Next, I consider the significance of swimming activity at higher oxygen concentration. The most plausible reason for the swimming behavior is to keep the larvae, which are negatively buoyant, from sinking out of the preferred depth zone in the sea. Day 1 larvae swim at an average angle of 39° upwards from the horizontal with no significant variation with oxygen concentration (Table 1). The large standard error is an indication of the wide spread of observed directions. The average swimming speed at this stage is 5.2±4.1 cm/s (Hunter 1972) and the average duration of a swimming bout (at oxygen concentration of 60-100%) is about 2.1 s (Figure 4). The average vertical component of the distance moved during a single bout is therefore

$$h_{up} = Vt \sin \alpha = 5.2 \cdot 2.1 \sin 39^\circ = 6.9 \text{ cm}. \quad (16)$$

The uncertainty in this value is large due to the standard errors in both the swimming angle and the average swimming speed, but it is probably accurate at least to an order of magnitude. Between swimming periods, the larvae sink at a speed of 0.12±0.03 cm/s (Hunter and Sanchez 1976). The average number of swimming bouts per 5-min period was found to be about 7 (Figure 4), i.e., giving an average sinking time of 43 s. This leads to a vertical distance of 5.2 cm, which is close enough to the value of 6.9 cm of Equation (16) to show that the swimming of day 1 larvae at high oxygen levels most probably is a depth-control mechanism.

The newly hatched (day 0) larvae present a different situation. Pelagic eggs are slightly positively buoyant (Blaxter 1969) while the chorion, which is shed during hatching, is somewhat negatively buoyant. Thus, while no measurements independent of the present ones exist, it is reasonable to assume that these newly hatched larva are approximately neutrally buoyant due to their large yolk sac. As the yolk is consumed, the specific gravity increases and the sinking rates for day 1 are obtained. The larvae are approximately neutrally buoyant during the first hours after hatching so that no net sinking or upward swimming is expected. Table 1 shows that this is actually the case at day 0, where the average direction is very close to horizontal and the large error indicates almost random swimming direction. Some upward swimming may be discerned at the very low O_2 concentration experiments (20% O_2). This may be a result of an inadvertent oxygen gradient in the tank or a phototactic response induced by the low oxygen concentration. Phototaxis is probably the means by which the older larvae choose swimming direction, and is directed upwards as light in the present experiments comes from the surface.

ACKNOWLEDGMENTS

This paper was written while I was a NRC-NOAA Senior Research Associate, on leave from the Department of Aeronautical Engineering, Technion, Haifa, Israel. I would like to thank John R. Hunter and Reuben Lasker for reading the manuscript and various discussions, E. H. Ahlstrom and Gail Theilacker for generously allowing me to use their unpublished data, and Bob Millman and Steve Lucas for help with the experiments.

LITERATURE CITED

ABRAMOWITZ, M., AND I. A. STEGUN (editors).
1965. Handbook of mathematical functions with formulas, graphs, and mathematical tables. Dover, N.Y., 1046 p.

BLAXTER, J. H. S.
1969. Development: eggs and larvae. *In* W. S. Hoar and D. J. Randall (editors), Fish physiology, Vol. 3, p. 177-252. Acad. Press, N.Y.

CRANK, J.
1975. The mathematics of diffusion. 2d ed. Clarendon Press, Oxf., 414 p.

DAYKIN, P. N.
1965. Application of mass transfer theory to the problem of respiration of fish eggs. J. Fish. Res. Board Can. 22:159-171.

HUNTER, J. R.
1972. Swimming and feeding behavior of larval anchovy *Engraulis mordax*. Fish. Bull., U.S. 70:821-838.

HUNTER, J. R., AND C. SANCHEZ.
1976. Diel changes in swim bladder inflation of the larvae of the northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 74:847-855.

LEVICH, V. G.
1962. Physiochemical hydrodynamics. Prentice-Hall, Inc., Englewood Cliffs, N.J., 700 p.

LILLELUND, K., AND R. LASKER.
1971. Laboratory studies of predation by marine copepods on fish larvae. Fish. Bull., U.S. 69:655-667.

O'BRIEN, R. N., S. VISAISOUK, R. RAINE, AND D. F. ALDERDICE.
1978. Natural convection: a mechanism for transporting oxygen to incubating salmon eggs. J. Fish. Res. Board Can. 35:1316-1321.

PROSSER, C.
1973. Comparative animal physiology. W. B. Saunders Co., N.Y., 966 p.

RILEY, J. P., AND G. SKIRROW.
1965. Chemical oceanography. Academic Press, N.Y., Vol. 1., 712 p.

WEIHS, D.
1980. Energetic significance of changes in swimming modes during growth of larval anchovy, *Engraulis mordax*. Fish. Bull., U.S. 77:597-604.

DESCRIPTIONS OF LARVAL SILVER PERCH, *BAIRDIELLA CHRYSOURA*, BANDED DRUM, *LARIMUS FASCIATUS*, AND STAR DRUM, *STELLIFER LANCEOLATUS* (SCIAENIDAE)[1, 2]

HOWARD POWLES[3]

ABSTRACT

This paper presents descriptions and illustrations of larval *Bairdiella chrysoura* (3.1-8.8 mm standard length), *Larimus fasciatus* (3.0-5.9 mm standard length), and *Stellifer lanceolatus* (2.8-15.1 mm standard length). *Larimus fasciatus* larvae are characterized by brain pigment, pectoral fin pigment, and early-developing pectoral fin rays. Larval *B. chrysoura* resemble *S. lanceolatus*, but *B. chrysoura* have a swath of expanded melanophores from nape to cleithral symphysis. These two species also can be differentiated by the sequence of melanophores in the midventral line posterior to the anus. Off the southeastern United States, *L. fasciatus* spawn in continental shelf waters from May to October, and *B. chrysoura* and *S. lanceolatus* spawn in coastal and estuarine waters during late spring and summer.

The perciform family Sciaenidae is represented by 18 species off the southeastern United States (Table 1). Taxonomy of adult Sciaenidae of the western North Atlantic has recently been revised by Chao (1978); nomenclature in the present paper follows Chao (1978) rather than Bailey et al. (1970). Studies of larval sciaenids of the east coast of the United States have been numerous; these have recently been summarized in several publications (Scotton et al. 1973; Johnson 1978; Powles and Stender 1978; Lippson and Moran[4].) Despite the number of larval studies, their quality has been uneven; for example, larval series now known to consist of more than one species have been described as single species (*Menticirrhus americanus* and *Stellifer lanceolatus* of Hildebrand and Cable 1934), damaged or distorted specimens have been illustrated and described (*Sciaenops ocellata* of Pearson 1929; *Leiostomus xanthurus* of Hildebrand and Cable 1930), and illustrations have differed from descriptions of larvae of the same species in the same publication (early *Stellifer lanceolatus* of Hildebrand and Cable 1934). Further, few detailed developmental series of morphometric, meristic, and pigmentation data have been published, making separation of larvae to species impossible in the early stages before complete development of fin elements. Thus, both description of undescribed or incompletely described larvae and redescription of larvae which have been poorly described in the literature are necessary to specific identification of sciaenid larvae.

The three species whose larvae are treated in this paper are generally similar in habitat and probably in ecology. They are small fishes (maximum total lengths 20-23 cm) of coastal and estuarine waters (Hildebrand and Schroeder 1928; Hoese and Moore 1977). None are important commercial or sport fish, but all are abundant in estuaries (Dahlberg 1972; Shealy et al. 1974) and on coastal shrimp grounds (Anderson 1968; Keiser 1976). Because of their abundance and small size, all may be important prey items for larger, predacious fishes.

Descriptions of larvae of all three species have been published. Kuntz (1915) described eggs and yolk-sac larvae of *Bairdiella chrysoura* from eggs obtained from a ripe female and further described larvae and early juveniles from plankton collections. Since he examined live or fresh material rather than Formalin-preserved[5] material, it is to be expected that body proportions and pigment characters of his series might differ from those in

[1]South Carolina Marine Resources Center Contribution No. 94.

[2]MARMAP Contribution No. 164.

[3]Marine Resources Research Institute, Charleston, S.C.; present address: Gouvernement du Canada, Pêches et Océans, Division des Sciences halieutiques, C.P. 15500, Québec, Canada G1K 7Y7.

[4]Lippson, A. J., and R. L. Moran. 1974. Manual for identification of early developmental stages of fishes of the Potomac River estuary. Md. Dep. Nat. Resour., Power Plant Siting Program, PPSP-MP-13:1-282.

[5]Reference to trade name does not imply endorsement by the National Marine Fisheries Service, NOAA.

Manuscript accepted August 1979.
FISHERY BULLETIN: VOL. 78, NO. 1, 1980.

larvae from preserved series. His description was cited by later authors (Hildebrand and Cable 1934; Scotton et al. 1973; Johnson 1978; Lippson and Moran see footnote 4) in compilations of larval

TABLE 1.—Reported meristics of South Atlantic Bight Sciaenidae. Counts in parentheses occur infrequently and semicolon indicates separate dorsal fins.

Species	Source[1]	Dorsal		Anal		Caudal procurrent	Vertebrae[2]	Gill rakers	
		Spines	Rays	Spines	Rays			Upper	Lower
Bairdiella chrysoura	1	X;I	19-23	II	8-10		12+13	7-8	14-16
	4	XI-XII	19-21	II	9-10				14-16
	5	XI;I	22	II	10			8	16
	7	XII	19-22	II	8-10	8-9, 5-8	11+14		
Cynoscion nebulosus	1	IX-X	25-28	II	10-11		(12)13+12(13)	2-3	7-9
	3		25		10-12		25		8
	4	X(XI);I	24-26	II	10-11				8
	5	X;I	25-27	II	10			4	7
	7	XI-XII	24-27	II	10-11		13+12		
	9		25-27		9-10	6-9, 5-7		4	6-8
C. nothus	1	X;I	26-30		8-10		15+12	3-4	8-10
	2		27-30(31)		8-9(10)		27(26)		12-14(15)
	3		24-28		8-10				12-14
	4	X;I	28-29	II	9				9
	5	X;I	27-29	II	9-10			4	9
	7	XI	28-30	II	9		14+13		
	9		26-29		9-11	7-8, 6-8			
C. regalis	1	X;I	26-29		11-13		(12)13+12(13)	4-5	10-13
	4	X;I	25-28	II	11-12				11-13
	5	X;I	26-29	II	11-13			5	11
	6	X-XI;I	24-29	II	10-12		14-15+10		
	7	XI	24-28	II	10-12	7-9, 5-7	13+12		
Equetus acuminatus	1	VIII-IX;I	37-41	II	7-8		10+15	5-6	9-14
	5	X;I	38-40	II	7			6	9
	7	X-XI	36-40	II	6-8		10+15		
	8	IX-X;I	37-40			7-8, 6-7			
E. lanceolatus	1	XII-XIII;I	47-55	II	6		10+15	5-6	10-13
	5	XIV-XVI;I	53	II	5			6	9
	7	XIII-XIV	46-50	II	6		10+15		
	8	XIII-XIV	49-55			7-8, 6-7			
E. punctatus	1	XI-XII;I	45-47	II	6-8		10+15	5	10-13
	5	XI-XII;I	46	II	6-7			6	11
	7	XIII	44-49	II	7-8		10+15		
	8	XI-XII;I	45-47			7, 5-7			
E. umbrosus	1	X-XI;I	38-40	II	7		10+15	4-6	10-12
	5	X;I	40	II	7				
	7	IX-XI	38-39	II	7	7-8, 7	10+15		
Larimus fasciatus	1	X;I	24-27				11+14	11-13	22-25
	4	X;I	24-27	II	6-8				23-25
	5	X;I	24-26	II	5-6			12	24
	7	XI-XII	25-27	II	6	6-7, 4-7	10+15		
Leiostomus xanthurus	1	IX;I	29-35	II	12-13		10+15	8-12	20-23
	4	X;I	30-34	II	12-13				22-23
	5	X;I	31	II	12			8	22
	7	XI-XII	29-32	II	12-13	6-8, 6-8	10+15		
Menticirrhus americanus	1	X;I	20-26	I	6-8		10+15	2-3	0-7
	4	X;I	24-27	I	7-8				6
	5	X;I	24-25	I	7				
	7	XI	24-26	II	7-8	8-9, 7	10+15		
M. littoralis	1	X-XI	19-26				10+15	3-5	0-8
	4	X;I	24-26	I	7				7-8
	5	X;I	23-25	I	7				7
	7	XI	24-25	II	7	7-8, 6	10+15		
M. saxatilis	1	X;I	22-27	I	7-9		10+15	3-5	0-7
	4	X;I	24-26	I	8-9				6
	5	X;I	26-27	I	8				
	7	XI	23-25	II	7-8	6-8, 6	10+15		
Micropogonias undulatus	1	X;I	27-30	II	8-9		10+15	8-10	14-18
	4	X;I	28-29	II	8				14-16
	5	X;I	28-29	II	7			7	16
	7	XI	28-29	II	8	8-9, 8	10+15		
Pogonias cromis	1	X;I	19-21	II	5-6		10+14	4-6	12-16
	4	X;I	20-22	II	6-7				14-16
	5	X;I	21	II	5-6			4	12
	7	XI	21-23	II	6	8-9, 7	10+14		
Sciaenops ocellata	1	X;I	23-25	II	8-9		10+15	4-5	7-9
	4	X;I	23-25	II	8				8-9
	5	X;I	24	II	8			5	7
	7	XI	23-25	II	7-8	8-10, 7-9	10+15		
Stellifer lanceolatus	1	XI-XII;I	20-24				11+14	10-13	22-23
	5	XI;I	20-23	II	7-8			13	22
	7	XII-XIII	21-24	II	7-9	7-9, 6-9	10+15		

TABLE 1.—Continued.

Species	Source[1]	Dorsal Spines	Dorsal Rays	Anal Spines	Anal Rays	Caudal procurrent	Vertebrae	Gill rakers Upper	Gill rakers Lower
Umbrina coroides	1	X,I	26-31	II	6		11+14	5-7	7-10
	4	X,I	29	II	6				11
	5	X,I	27-28	II	6-7			5	9

[1]Sources:
1. Chao 1978
2. Ginsburg 1929
3. Hildebrand and Cable 1934
4. Hildebrand and Schroeder 1928
5. Jordan and Evermann 1896
6. Lippson and Moran (see text footnote 4)
7. Miller and Jorgensen 1973
8. Randall 1968
9. Welsh and Breder 1923.

[2]Includes urostyle.

sciaenids. Jannke[6] illustrated *B. chrysoura* of 2.0 and 5.0 mm SL (standard length). Hildebrand and Cable (1934) described a series identified as *Larimus fasciatus*. Although there is some disagreement between illustrations and descriptions of early larvae in this work, the series appears to represent a single species and to be correctly identified. Hildebrand and Cable also described larvae and juveniles identified as *Stellifer lanceolatus*. Their early larvae represent a mixed series; larvae <4 mm long had pectoral fin pigment and developed pectoral rays, but larvae >4.5 mm long had no pectoral pigment and pectoral rays that developed at ≥5.6 mm. Body proportions also changed between 4.0 and 4.5 mm. Their series appears coherent and correctly identified at lengths ≥5.6 mm. There were also some discrepancies between drawings and descriptions of early stages in their paper.

The purpose of the present paper is to redescribe larvae of these three species and to summarize characters for differentiating between the three species. In addition, notes are given on time and place of larval collections and on separation of larvae of these three species from those of other marine sciaenids of the southeastern United States.

METHODS

Approximately 50 specimens of each species were examined. Descriptions are based on the following numbers of specimens: silver perch, *Bairdiella chrysoura*, 21; banded drum, *Larimus fasciatus*, 21; star drum, *Stellifer lanceolatus*, 26.

Specimens on which descriptions were based were collected from continental shelf waters of the South Atlantic Bight, estuaries and tidal passes of South Carolina, and the Cape Fear River estuary of North Carolina. Those from continental shelf waters were collected with Boothbay neuston nets (mouth 1 m high × 2 m wide, mesh size 0.947 mm, tow velocity 2.6 m/s), MARMAP neuston nets (mouth 0.5 × 1.0 m, mesh size 0.505 mm, tow velocity 1.0 m/s), and 60 cm bongo nets (mesh size 0.505 mm, towing velocity 0.8 m/s) towed in a double oblique pattern between surface and bottom or 200 m depth. Specimens from South Carolina estuaries were collected with 0.5 m diameter conical nets (mesh size 0.571 mm, towing velocity 1.3-1.5 m/s) towed at surface or bottom. South Carolina tidal passes were sampled with 1.0 m mouth diameter plankton nets (mesh size 0.571 mm) moored to bridges or piers and fished near bottom for 1 h at early or middle flood tide. Specimens from the Cape Fear River estuary were collected with 1.0 m mouth diameter conical nets (mesh size 0.760 mm) towed at surface at 0.5 m/s. The number of samples available from each area except the Cape Fear River estuary by month (Table 2) provides an estimate of seasonal and areal effort distribution for comparison with data on time and place of capture of larvae. Tidal pass sampling was not carried out from August to January, and estuarine samples from August to December were not available. All specimens were preserved in 2% formaldehyde buffered by saturating with borax. Specimens from continen-

TABLE 2.—Numbers of plankton samples from South Carolina estuaries (1974), South Carolina tidal passes (1976), and the South Atlantic Bight continental shelf (1973-76) that were sorted for larval Sciaenidae.

Month	Estuaries Surface	Estuaries Bottom	Tidal passes	Continental shelf Neuston	Continental shelf Bongo
Jan.	33	30	—	30	30
Feb.	17	14	2	30	30
Mar.	17	14	1	47	47
Apr.	33	28	1	52	38
May	19	17	2	48	48
June	17	17	5	—	—
July	16	16	8	—	—
Aug.	—	—	—	40	37
Sept.	—	—	—	39	1
Oct.	—	—	—	10	11
Nov.	—	—	—	31	16

[6]Jannke, T. E. 1971. Abundance of young sciaenid fishes in Everglades National Park, Fla., in relation to season and other variables. Univ. Miami Sea Grant Tech. Bull. 11:1-128.

tal shelf waters were initially fixed by immersing net cod ends in 8% formaldehyde for 2 min immediately following net washdown.

Measurements were made on the left side of the body, by ocular micrometer on a dissecting microscope. All measurements were made along or perpendicular to the body midline. Measurements are defined as follows:

Notochord length (NL) — symphysis of upper jaw to tip of notochord (measured in preflexion larvae).

Standard length (SL) — symphysis of upper jaw to posterior edge of hypurals (measured in larvae undergoing notochord flexion and in postflexion larvae).

Snout length — symphysis of upper jaw to anterior margin of eye.

Eye diameter — horizontal diameter of eye.

Head length — symphysis of upper jaw to posterior margin of opercular membrane.

Preanus length — symphysis of upper jaw to posterior margin of anus.

Snout to origin of spinous dorsal fin — symphysis of upper jaw to anterior margin of first developed dorsal spine base.

Snout to origin of soft dorsal fin — symphysis of upper jaw to anterior margin of first developed dorsal ray base.

Snout to dorsal fin termination — symphysis of upper jaw to posterior margin of last developed dorsal ray base.

Snout to anal fin origin — symphysis of upper jaw to anterior margin of first developed anal element base.

Snout to anal fin termination — symphysis of upper jaw to posterior margin of last developed anal ray base.

Anus to anal fin — posterior margin of anus to first developed anal element base.

Snout to pelvic fin insertion — symphysis of upper jaw to anterior margin of base of pelvic fin.

Depth at cleithral symphysis — vertical distance between dorsal margin of body and ventral symphysis of cleithra.

Depth at caudal peduncle — least vertical distance between dorsal and ventral margins of body in the area posterior to the terminal dorsal and anal fin rays and anterior to the hypural bones.

Fin counts include all elements of which any part (including pterygiophore) was developed. Counts were made in unstained specimens since the primary purpose of the study was to permit identification of specimens from field collections. Unless otherwise stated, lengths referred to in this paper are standard lengths.

Data on occurrences of larval *Larimus fasciatus* in plankton tows from continental shelf waters between Martha's Vineyard, Mass., and Palm Beach, Fla., were provided by Peter Berrien (Fisheries Biologist, Northeast Fisheries Center Sandy Hook Laboratory, National Marine Fisheries Service, NOAA, Highlands, NJ 07732). Collection methods and station distribution are given in Clark et al. (1969, 1970).

RESULTS

Bairdiella chrysoura

Morphology. Body proportions change gradually during larval development (Table 3). Body depth at the cleithral symphysis increases slightly with growth and is >30% SL in all specimens examined. Caudal peduncle depth remains constant through development. Preanus length increases from 40-45% SL in preflexion and flexion larvae to >50% SL at ≥5.7 mm. Positions of the dorsal, anal, and pelvic fins remain quite constant as the fins develop, whereas the decrease in length of the anus-anal fin gap corresponds to the increase in preanus length. Snout length and eye diameter change little during development, whereas head length increases from 27-31% NL or SL in preflexion and flexion larvae to 35% SL in larvae 4.9 mm.

Lateral and marginal preopercular spines are present throughout the series, becoming more numerous with growth until a maximum of five lateral and four marginal spines are present at 7.0-8.8 mm. A single posttemporal spine is present at 5.0-7.7 mm, and two such spines are present at 8.8 mm.

Fin development. The pectoral fin is present in all specimens examined; ray development begins at 5.7 mm and 16 rays are present by 8.8 mm (Table 4). Notochord flexion occurs at 4.1-4.4 mm SL. Development of caudal rays begins at the same time as notochord flexion. The full complement of principal rays is developed soon after completion of notochord flexion. Procurrent caudal rays begin to form at 5.7 mm and an incomplete procurrent ray count is present at 8.8 mm. The soft dorsal and anal fins begin ray development at the start of

TABLE 3.—Body proportions (percentage of NL or SL) of larval *Bairdiella chrysoura*. Specimens between dashed lines undergoing notochord flexion; lengths are NL above upper dashed line, SL below.

NL or SL (mm)	Snout length	Eye diameter	Head length	Preanus length	Snout to spinous dorsal origin	Snout to soft dorsal origin	Snout to soft dorsal termination	Anus to anal fin	Snout to anal fin origin	Snout to anal fin termination	Snout to pelvic fin insertion	Body depth at cleithrum	Caudal peduncle depth
3.1	8.7	10.0	30.0	42.5	-	-	-	-	-	-	-	35.0	-
3.5	6.8	10.3	31.0	41.3	-	-	-	-	-	-	-	31.0	-
3.6	7.4	9.8	27.6	40.4	-	-	-	-	-	-	-	30.8	-
3.7	7.4	10.6	30.8	41.4	-	-	-	-	-	-	-	31.9	-
3.7	6.3	10.5	27.3	40.0	-	-	-	-	-	-	-	32.1	-
3.8	7.4	9.5	28.7	44.6	-	-	-	-	-	-	-	32.9	-
4.1	7.2	11.7	31.5	46.8	-	54.1	77.5	15.4	62.2	74.8	-	35.1	8.1
4.4	10.6	12.4	37.2	48.7	42.5	61.9	83.2	17.7	66.4	81.4	-	37.2	9.7
4.4	8.9	11.1	30.3	44.6	40.1	57.1	76.7	21.7	66.3	80.3	-	33.9	7.1
4.8	9.8	11.4	31.1	45.9	39.3	57.3	78.6	16.3	62.2	73.7	-	33.6	6.5
4.9	7.9	10.3	37.3	48.4	38.9	57.1	82.5	16.7	65.1	80.2	35.7	36.5	10.3
5.0	8.6	10.9	35.2	49.2	39.9	57.8	83.6	17.9	67.1	80.5	35.9	36.7	10.1
5.7	8.6	11.4	35.7	48.6	38.6	60.0	82.9	17.1	65.7	80.0	35.7	37.1	11.4
5.7	8.6	11.4	35.7	51.4	37.1	58.6	82.8	11.4	62.8	81.4	37.1	37.1	11.4
7.0	7.0	11.6	37.2	57.0	37.2	59.3	82.5	8.1	65.1	80.2	38.4	37.2	11.6
7.5	10.9	10.9	35.8	55.4	38.1	59.8	81.5	7.6	63.0	78.3	35.8	35.8	10.9
7.5	8.7	10.9	36.9	53.3	39.1	57.6	83.7	11.9	65.2	79.3	35.8	35.8	8.7
7.7	10.6	10.6	38.3	58.5	43.6	59.6	82.9	9.6	68.1	80.8	40.4	37.2	10.6
8.8	9.3	11.2	36.4	56.1	39.3	59.8	85.0	8.4	64.5	79.5	39.3	36.4	10.3

TABLE 4.—Fin element counts of larval *Bairdiella chrysoura*. Specimens between dashed lines undergoing notochord flexion; lengths are NL above upper dashed line, SL below.

NL or SL (mm)	Spinous dorsal	Soft dorsal	Anal	Pectoral[1]	Pelvic	Caudal principal	Caudal procurrent
3.1				+			
3.5				+			
3.6				+			
3.7			-	+		-	
3.7			-	+		-	
3.8				+			
4.1		14	6	+		7-6	
4.4		15	8	+		7-7	
4.4		18	6	+		7-7	
4.8		20	10	-	-	8-7	
4.9	-	19	I.9	-		9-8	
5.0		I.21	I.9	-		9-8	
5.7	XI	21	II.9	+	3	9-8	3.1
5.7	XI	I.21	II.9	6	I.2	9-8	
7.0	XI	I.21	II.9	11	I.5	9-8	4.3
7.5	XI	I.21	II.9	12	I.5	9-8	5.4
7.5	XI	I.22	II.9	8	I.5	9-8	4.4
7.7	XI	I.21	II.9	12	I.5	9-8	5.4
8.8	XI	I.22	II.9	16	I.5	9-8	6.5

[1] + = fin present, no developed elements

notochord flexion and attain adult complements at ≥4.8 mm. The spinous dorsal begins development between 5.0 and 5.7 mm; spine development is rapid, with the adult complement present at 5.7 mm. Pelvic fins are first present at 5.7 mm and adult element complements are present at ≥7.0 mm.

Pigmentation. Larvae are characterized by an oblique swath of internal and external pigment, paralleling the cleithrum, from nape to cleithral symphysis (Figure 1). Melanophores of several areas constitute this swath: in the musculature of the nape, on the anterior and dorsal surfaces of the visceral mass, ventral to the brain, and on the ventral body surface. In small larvae (<5.0 mm), melanophores in these areas are usually expanded, so that a continuous swath of pigment is formed. Occasionally melanophores may be contracted, but are always present in the areas listed. In large larvae (≥5.0 mm), melanophores of these areas are more frequently contracted than in smaller larvae, and thickening of the body wall begins to obscure some of the swath pigment.

Pigment of the ventral midline of the tail begins as a continuous row of small melanophores in the smallest larvae and develops into a characteristic sequence of melanophores with growth. About 10 melanophores are present at 3.1-3.8 mm; one of these (two-thirds of the distance from anus to notochord tip) is larger than the others. In the dorsal midline of the tail, a few specimens ≤3.5 mm NL have a small melanophore dorsal to the large melanophore of the ventral midline. At ≥4.1 mm, melanophores of the ventral row are placed as follows: one or two anterior to the anal base, one at the origin of the anal fin, one at its termination, and three or four posterior to the anal fin. In most specimens ≥7.0 mm, no pigment is present anterior to the anal base, but the rest of the sequence remains, and small melanophores begin to appear at the bases of individual rays.

Other head and visceral mass pigmentation characterizes these larvae. A melanophore is present at the angle of the lower jaw throughout the series. Pigment is present at the tip of the

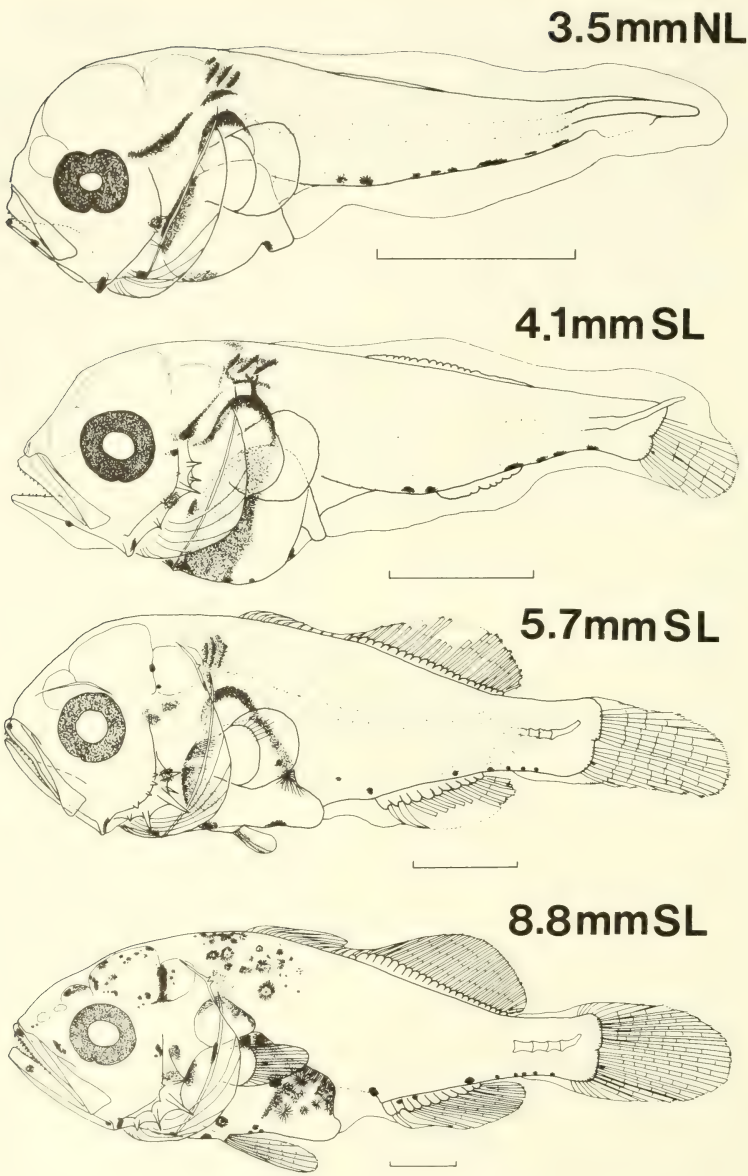


FIGURE 1.—Larval *Bairdiella chrysoura*. Scale equals 1 mm.

premaxillary at ≥5.7 mm and at the tip of the lower jaw at ≥7.5 mm. A melanophore is usually present on the medial surface of each dentary at 3.1-7.0 mm, while at ≥7.5 mm, one or several melanophores consistently occur in this position. Melanophores are present above the anterior part of the midbrain, and above the eye, at ≥7.0 mm. Melanophores are present on the surface of the midbrain at its junction with the hindbrain at ≥5.7 mm, and on the dorsal surface of the forebrain at ≥7.7 mm. Two melanophores occur in the midventral line on the ventral surface of the visceral mass: one midway between the cleithral symphysis and the anus (between the pelvic fin bases when these are developed), present at ≥3.3 mm, and another on the anterioventral surface of the anus, present at 3.1-5.0 mm. A melanophore midway between these is occasionally present at 3.5-4.7 mm and always present at ≥4.8 mm. On the posterior surface of the visceral mass, above the anus, a melanophore is present at ≥4.9 mm; this melanophore becomes increasingly branched and dark at ≥5.7 mm.

Body surface pigment increases in extent in late larvae (≥7.0 mm). This includes a cluster of melanophores in the dorsal midline anterior to the spinous dorsal fin, a group of melanophores ventral to this cluster, a group on the dorsal surface of the head, and a group on the lateral surface of the visceral mass.

Identification of the series. This series was identified as *B. chrysoura* by fin ray counts, pigmentation, caudal fin shape, and similarity to a published description. Fin ray counts (dorsal 21-22, anal 9) of late larvae in the series could have been attributed to *Menticirrhus americanus, M. saxatilis*, or *Stellifer lanceolatus* as well as *B. chrysoura*. A series of *Menticirrhus* larvae (identified by presence of a single mental barbel at ≥9.2 mm, tentatively as *M. americanus*), which I have examined, is characterized by heavy and extensive body pigment, and the absence of such pigment in larvae of the series described here indicated that it was *B. chrysoura* rather than *M. americanus*. Heavy body pigmentation has been described for *M. americanus* (Hildebrand and Cable 1934) and *M. saxatilis* (Scotton et al. 1973). Although species identifications in those descriptions may not be accurate, heavy body pigmentation is probably characteristic of larvae of the genus *Menticirrhus*. Caudal fin shape distinguished larvae of the series here described from larval *S. lanceolatus*. Late larvae of this series have the broadly rounded caudal fin characteristic of *B. chrysoura* (Hildebrand and Schroeder 1928; Dahlberg 1975) while late larvae of *S. lanceolatus* have the lanceolate caudal fin characteristic of the adult. Finally, larvae of my series are similar in major characters (the swath of pigment between head and visceral mass, midventral pigment posterior to the anus) to the larvae described by Kuntz (1915), which were apparently correctly identified.

Spawning season and area. Larval *B. chrysoura* occurred in six surface and six bottom tows in May and in five surface and five bottom tows in June 1974 in South Carolina estuaries. None occurred between January and April or in July. In South Carolina tidal passes, larvae occurred in two May samples, one June sample, and one July sample, and did not occur between February and April. A single specimen was taken in continental shelf waters, in a bongo net tow made in 31 m on 8 April 1974 (Figure 2). Thus spawning appears to occur primarily in coastal and estuarine waters of the southeastern United States, at least from April through July. Spawning may occur later in the year, but no samples after July from coastal and estuarine waters were examined.

Larimus fasciatus

Morphology. Body proportions change little during development (Table 5). The larvae are deep bodied (depth at cleithral symphysis >35% SL, except for a 3.8 mm specimen). Preanus length is >50% SL in all specimens but one. Positions of the fins change little during development. Anus to anal fin distance is variable in length, <6% SL in most larvae but with a maximum value of 10.2% SL. Caudal peduncle depth increases with development, from <9% SL at ≤4.2 mm to >9% SL in most larger specimens.

Preopercular spines are present in all larvae. Lateral spines are smaller than marginal spines, and numbers in both series increase with growth. One or two small posttemporal spines and a low, spinous supraorbital ridge are present at ≥5.5 mm.

Fin development. The pectoral fins are present throughout development (Table 6). Pectoral elements are first present at ≥4.0 mm; elements are incomplete at 5.9 mm, the largest larva available

TABLE 5.—Body proportions (percentage of NL or SL) of larval *Larimus fasciatus*. Specimens between dashed lines are undergoing notochord flexion. Lengths are NL above upper dashed line, SL below.

NL or SL (mm)	Snout length	Eye diameter	Head length	Preanus length	Snout to spinous dorsal origin	Snout to soft dorsal origin	Snout to soft dorsal termination	Anus to anal fin	Snout to anal fin origin	Snout to anal fin termination	Snout to pelvic fin insertion	Body depth at cleithrum	Caudal peduncle depth
3.0	10.4	10.4	33.8	53.2	–	50.6	68.8	–	–	–	–	50.6	6.5
3.2	9.6	12.0	36.1	53.0	–	–	–	–	–	–	–	39.8	7.2
3.6	10.9	13.0	35.9	55.4	41.3	53.3	76.1	4.4	59.8	71.7	39.1	39.1	8.7
3.8	9.2	12.2	34.7	49.0	–	–	–	10.2	59.2	70.4	–	33.7	6.1
4.0	10.8	12.8	38.8	56.8	–	52.0	76.8	4.0	60.8	74.4	35.6	39.6	9.2
4.2	7.3	11.9	36.7	54.1	36.7	50.5	81.7	5.5	59.6	71.6	37.6	37.6	8.3
4.3	10.1	13.8	40.4	57.8	39.4	55.0	81.7	5.5	63.3	74.3	35.8	40.4	9.2
4.3	8.2	12.7	38.2	57.3	41.8	54.5	85.5	3.6	60.9	71.8	39.1	40.9	8.2
4.4	9.7	13.3	38.1	58.4	43.4	58.4	89.4	8.9	67.3	75.2	36.3	42.5	10.6
4.5	9.6	13.2	36.8	54.4	40.4	49.1	86.0	9.6	64.0	76.3	36.0	37.7	8.8
4.8	8.1	13.8	41.5	65.0	41.5	58.5	87.0	4.1	69.1	78.9	40.7	41.5	10.6
4.9	10.3	14.3	37.3	61.9	40.5	57.1	87.3	0.8	62.7	77.0	39.7	44.4	10.3
5.0	9.4	15.0	40.2	58.3	39.4	55.1	87.4	4.7	63.0	75.6	39.4	46.5	11.0
5.5	7.5	13.4	35.8	59.7	41.8	56.7	89.6	4.5	64.2	77.6	37.3	44.8	11.9
5.7	10.3	14.5	37.9	60.0	38.6	57.9	89.0	5.5	65.5	79.3	37.2	44.1	11.0
5.8	9.9	12.7	38.0	60.6	42.3	59.2	87.3	1.6	62.0	74.6	39.4	45.1	11.3
5.9	12.5	13.9	40.3	59.7	44.4	59.7	87.5	5.6	65.3	76.4	37.5	43.1	9.7

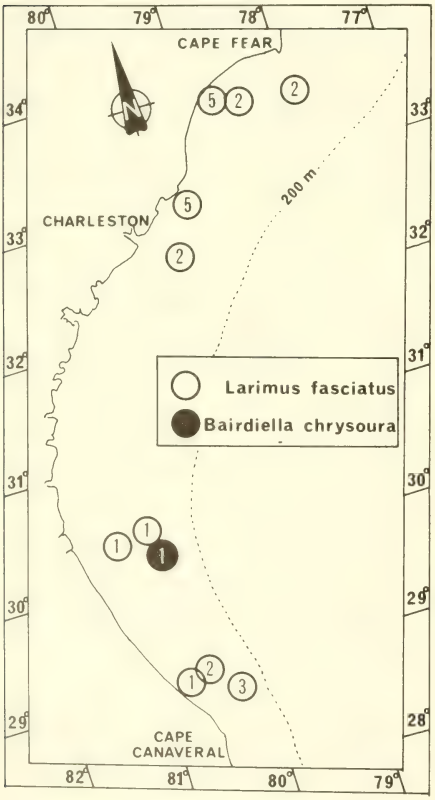


FIGURE 2.—Occurrence of larval *Bairdiella chrysoura* and *Larimus fasciatus* in South Carolina-MARMAP plankton tows in continental shelf waters of the South Atlantic Bight. Numbers indicate numbers of larvae at stations.

TABLE 6.—Fin element counts in larval *Larimus fasciatus*. Specimens between dashed lines are undergoing notochord flexion. Lengths are above upper dashed line, SL below.

NL or SL (mm)	Spinous dorsal	Soft dorsal	Anal	Pectoral[1]	Pelvic[1]	Caudal principal	Caudal procurrent
3.0	–	–		+	–	–	–
3.2	–	–	–	+	–	–	–
3.6	–	16	5	+	+	6+5	–
3.8	–	18	–	+	–	3+3	–
4.0		19	7	10	+	9+8	–
4.2	–	16	7	+	+	8+6	–
4.3	–	15	6	7	+	4+5	–
4.3	–	20	7	6	+	8+7	–
4.4	IX	27	II,6	11	I,4	9+8	–
4.5	III	22	7	10	+	8+6	–
4.8	X	25	6	10	+	9+7	–
4.9	X	27	II,6	12	I,3	9+8	–
5.0	X	26	II,6	10	I,1	9+8	–
5.5	X	27	II,6	15	I,5	9+8	0,1
5.7	X	27	II,6	14	I,4	9+8	0,1
5.8	XI	26	II,6	16	I,5	9+8	1,2
5.9	IX	27	II,6	15	I,5	9+8	2,2

[1] + = fin present, no developed elements.

(adult complement 17 in nine adults, 16 in one, all from South Carolina waters). Caudal flexion is occurring in specimens of 3.6-4.0 mm. Principal caudal rays are first seen in flexion specimens and are usually complete after 4.9 mm. Procurrent caudal rays appear at 5.5 mm and are incomplete in the largest specimen available. The soft dorsal fin base is present in the smallest larva, with no discernible elements; pterygiophores are countable at 3.6 mm and rays are consistently complete at ≥4.8 mm. Dorsal spines first appear at 4.4 mm

and are complete in one specimen at 5.8 mm. The anal fin is first present at 3.6 mm; the complete anal ray complement is present at ≥4.0 mm and anal spines are complete consistently at 4.9 mm. The pelvic fin bud is first present at 3.6 mm, and the complete element complement consistently present at ≥5.8 mm.

Pigmentation. Characteristic pigment patterns of the brain and pectoral fin are useful for identifying larval *L. fasciatus* (Figure 3). Melanophores are present on the anterior surface of the forebrain, the anterior and posterior surfaces of the midbrain, the posterodorsal surface of the hindbrain, and the ventral surface of the brain posterior to the eye, throughout the available series. The midbrain pigment appears to ring the midbrain when viewed from dorsally. The pectoral fin base and membrane are heavily pigmented throughout the series. Pigment in the membrane, diffuse in small larvae, is present between the rays when these are developed (≥4.3 mm). An expanded melanophore is present on the visceral mass just ventral to the pectoral fin base throughout the series; two or more melanophores may occur here at ≥4.2 mm.

Other head pigment includes two to four melanophores on the gular isthmus between the lower jaw rami, melanophores on the preoperculum posterior to the eye, a melanophore at the angle of the lower jaw, and one anterior to the cleithral symphysis.

In the ventral midline of the visceral mass, early larvae have three melanophores: one posterior to the cleithral symphysis (between pelvic fin bases when present), one midway between cleithral symphysis and anus, and one on the anteroventral surface of the anus. At ≥3.6 mm, the anus melanophore is absent, and at ≥4.5 mm, two or three melanophores may occur at the other two ventral midline locations. The anterior, dorsal, and posterior surfaces of the visceral mass are pigmented throughout the series, and at ≥5.0 mm, melanophores appear and increase in numbers on the lateral surface of the visceral mass.

In the ventral midline posterior to the anus, a row of six melanophores is present in the smallest larva (3.0 mm), the fifth of which, midway between the anus and notochord tip, is larger than the others. At ≥3.2 mm, two melanophores occur in the ventral midline, one at the position of the large melanophore of the original series (at the posterior end of the anal base when developed) and one anterior to this (just posterior to the anterior end of the anal base when developed).

In the dorsal midline, a melanophore is present anterior to the origin of the finfold or spinous dorsal at ≥3.8 mm; two or three melanophores may be present here at ≥4.5 mm. Two melanophores, one on either side of the midline, are present midway along the spinous dorsal base at ≥4.8 mm, and a similar pair of melanophores is present two-thirds of the distance along the soft dorsal base at ≥5.9 mm.

On the lateral surface of the body, between the spinous dorsal base and the visceral mass, melanophores appear at 4.4 mm and increase in number with growth.

Identification of the series. This larval series was identified as *L. fasciatus* by dorsal and anal fin ray counts, pigmentation, and by correspondence with a published description of late larval and early juvenile stages. Fin ray counts (dorsal 26-27, anal 6) observed in late larvae of this series could only have been of *L. fasciatus* or *M. americanus* (Table 1). The absence of heavy, extensive body pigmentation characteristic of *Menticirrhus* larvae indicated that the series described here was *L. fasciatus* rather than *M. americanus*. The pectoral fin pigment of the series here described is similar to that of *L. fasciatus* late larvae and early juveniles described by Hildebrand and Cable (1934). Although descriptions of early larvae in that paper are inadequate, late larvae (≥10.5 mm) and juveniles represent a coherent series apparently correctly identified.

Spawning season and area. No larval *L. fasciatus* were present in samples from South Carolina estuaries or tidal passes throughout the months sampled, January-July. In MARMAP tows in shelf waters, larvae were taken in April-May 1974, August-September 1974, and September 1975; larvae were most frequently taken on the inner two-thirds of the continental shelf and occurred from Cape Canaveral to Cape Fear (Figure 2). Information from plankton collections made by personnel of Northeast Fisheries Center Sandy Hook Laboratory (Figure 4) shows larval *L. fasciatus* to have been distributed across the width of the continental shelf and as far south as lat. 27°43′ N. Large collections of larvae (6-18 specimens) were common off northern Florida and southern Georgia. Larval *L. fasciatus* were taken in cruises made during May, July, and October off

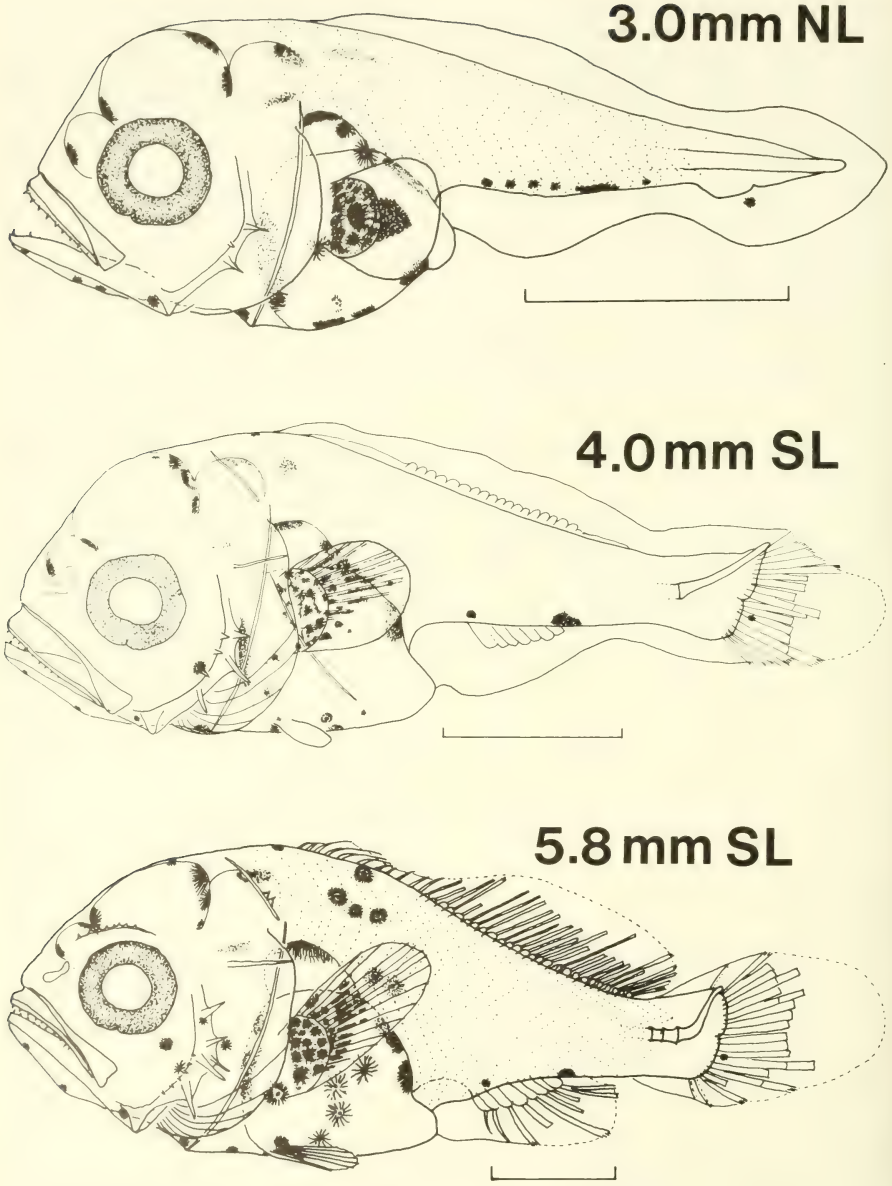


FIGURE 3.—Larval *Larimus fasciatus*. Scale equals 1 mm.

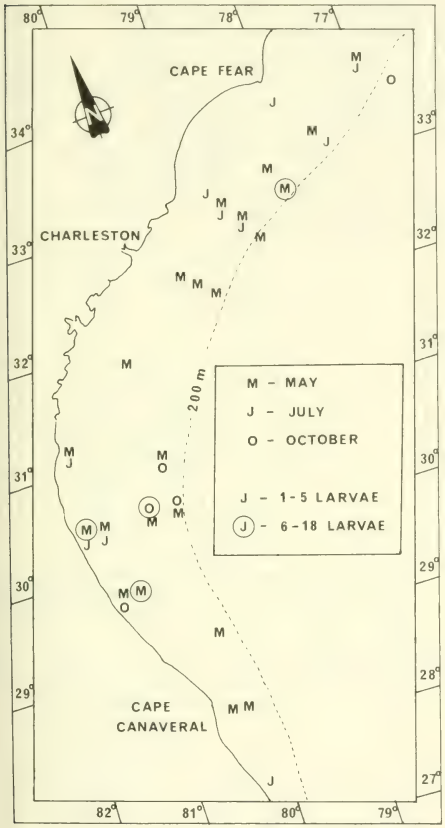


FIGURE 4.—Distribution of captures of larval *Larimus fasciatus* during plankton tows conducted by personnel of Northeast Fisheries Center Sandy Hook Laboratory off the southeastern United States (data supplied by Peter Berrien, Fishery Biologist, Northeast Fisheries Center Sandy Hook Laboratory, NMFS, NOAA, Highlands, NJ 07732).

the southeast United States; larvae were absent from the cruises made in January-February. On cruises made north of Cape Lookout, N.C., by Northeast Fisheries Center Sandy Hook Laboratory personnel, larval *L. fasciatus* were found as far north as lat. 36°22′ N (just south of the mouth of Chesapeake Bay); larvae were approximately as widely distributed and as abundant in continental shelf waters between Cape Lookout and Chesapeake Bay as off the southeastern United States (Berrien[7]). Larval *L. fasciatus* were collected in April to June and August to October on these "northern section" cruises.

Stellifer lanceolatus

Morphology. Body proportions change little during larval development (Table 7). The body is fairly deep (depth at cleithral symphysis 34-41% SL in most specimens). Preanus length, 40-50% SL through most of the series, increases to 55% SL in most late larvae (≥10.2 mm SL). Fins develop at the adult positions. The anus-anal fin gap, 12-20% SL in most specimens <8 mm, decreases with an increase in preanus length in larvae >10 mm. Head length increases slightly with development to the late larval stages; snout length and eye diameter change little over the size range available. Depth of the caudal peduncle increases slightly before and during notochord flexion and remains constant after flexion is complete.

Small lateral and large marginal preopercular spines are present throughout the series, as are premaxillary and dentary teeth. A posttemporal spine is present at 5.1-7.8 mm; at ≥10.2 mm a "scale bone" with four spinous projections is present in the posttemporal region.

Fin development. The pectoral fin, present throughout the series, first has elements at 6.9 mm and has the complete ray complement consistently at ≥14.0 mm, although the complete ray complement may be present in smaller larvae (Table 8). Notochord flexion occurs between 3.3 and 4.3 mm. Principal caudal rays are present in one preflexion larva and are consistently present during and after flexion; the adult complement is present at ≥5.5 mm. Procurrent caudal rays first appear at 5.1 mm and are complete at ≥10.2 mm. Bases of the soft dorsal and anal fins are present, with no discernible elements, in two preflexion specimens, and are consistently present with developed pterygiophores in flexion and postflexion specimens. Complete anal ray counts occur at ≥3.3 mm, and complete anal spine complements at ≥5.5 mm. Dorsal ray complements are consistently complete at ≥5.5 mm although complete counts may occur at 4.5 mm. Dorsal spines are occasionally seen at 4.5-5.8 mm and are consis-

[7]Peter L. Berrien, Fishery Biologist, Northeast Fisheries Center Sandy Hook Laboratory, National Marine Fisheries Service, NOAA, Highlands, NJ 07732, pers. commun. June 1979.

TABLE 7.—Body proportions (percentage of NL or SL) of larval and juvenile *Stellifer lanceolatus*. Specimens between dashed lines are undergoing notochord flexion. Lengths are NL above upper dashed line, SL below.

NL or SL (mm)	Snout length	Eye diameter	Head length	Preanus length	Snout to spinous dorsal origin	Snout to soft dorsal origin	Snout to soft dorsal termination	Anus to anal fin	Snout to anal fin origin	Snout to anal fin termination	Snout to pelvic fin insertion	Body depth at cleithrum	Caudal peduncle depth
2.8	8.2	11.0	30.1	45.2	–	–	–	–	–	–	–	37.0	6.8
2.9	9.3	10.7	33.3	45.3	–	50.6	66.7	13.3	58.6	69.3	–	37.3	6.7
3.1	8.8	11.4	32.9	41.7	–	48.0	69.6	21.5	63.2	74.6	–	38.0	7.6
3.1	8.9	11.4	35.4	41.8	–	–	–	–	–	–	–	35.4	7.6
3.5	6.6	11.0	27.4	39.5	–	–	–	–	–	–	–	34.1	6.6
3.3	5.9	12.9	34.1	47.1	–	61.2	90.5	18.7	65.8	84.7	–	41.2	9.4
3.4	6.9	11.5	36.8	46.0	–	51.7	77.0	13.8	59.8	74.7	–	40.3	8.1
3.8	7.2	9.3	27.8	41.2	–	49.4	70.1	17.6	58.8	73.2	–	35.0	6.2
4.1	7.5	11.3	31.1	45.3	39.6	54.7	86.8	15.1	60.4	79.2	–	39.6	10.4
4.3	8.2	11.8	31.8	45.5	–	53.6	81.8	16.3	61.8	78.2	–	38.2	10.9
4.5	8.7	11.3	34.7	48.7	35.7	57.4	86.1	12.1	60.8	77.3	37.4	40.8	11.3
4.9	8.7	9.5	32.5	42.9	36.5	55.6	83.3	19.0	61.9	80.2	30.2	36.5	8.7
5.1	9.7	12.9	35.5	48.4	35.5	56.4	87.1	12.9	61.3	77.4	35.5	38.7	9.7
5.5	7.5	10.4	32.8	43.3	32.8	49.3	80.6	14.9	58.2	76.1	–	35.8	9.0
5.5	9.0	10.4	31.3	47.8	34.3	52.2	90.0	11.9	59.7	79.1	–	37.3	9.0
5.8	7.0	14.1	31.0	43.7	35.2	50.7	84.5	15.5	59.2	76.1	32.4	32.4	8.5
6.2	8.0	8.0	32.0	46.7	34.7	54.7	82.7	12.0	58.7	76.0	32.0	36.0	9.3
6.9	8.3	9.5	34.5	45.2	36.9	54.7	82.1	14.3	59.5	76.2	29.7	33.3	9.5
7.4	10.0	10.0	37.8	54.4	41.1	56.7	84.4	8.9	63.3	77.8	41.1	37.8	10.0
7.6	8.6	8.6	35.4	47.3	37.6	55.9	86.0	11.8	59.1	76.3	31.1	34.4	9.7
7.8	7.4	9.5	32.6	45.3	35.8	53.6	83.2	12.6	57.9	79.0	30.5	35.8	9.5
10.2	8.8	9.6	38.4	55.2	40.0	59.2	85.6	8.8	64.0	79.2	38.4	36.0	5.6
13.1	10.3	9.0	38.5	57.6	38.5	58.9	85.9	6.5	64.1	78.2	39.7	35.8	9.0
13.9	9.6	7.2	39.7	54.2	38.5	59.0	85.5	9.7	63.9	78.3	36.1	33.7	9.6
14.0	9.0	9.0	37.3	55.4	36.2	54.1	85.5	8.4	63.8	78.3	38.5	33.7	9.6
15.1	10.0	8.9	38.9	57.8	36.7	55.5	84.5	7.7	65.5	77.7	38.9	33.3	8.9

tently present at 6.2 mm; the adult complement is consistently present at ≥10.2 mm. The pelvic fin bud is first present at 4.9 mm and is consistently present at ≥6.2 mm; adult element complements are present at ≥6.9 mm.

Pigmentation. Pigmentation of the body posterior to the anus is of particular value in identification of larval *S. lanceolatus* (Figure 5). In the ventral midline, small larvae (≤3.1 mm) have a row of five or six melanophores between the anus and the notochord tip; one or two of these, two-thirds of the distance from anus to notochord tip, are larger than the others. In larger specimens, an expanded melanophore is present two-thirds of the distance from anus to notochord tip (at the posterior end of the anal base when developed); this melanophore branches dorsally, often as far as the midlateral line. In some specimens (as shown, Figure 5) two expanded, branching melanophores are present at the posterior end of the anal fin base. In most specimens ≥3.1 mm, a melanophore is present (at the anterior end of the anal base when developed) anterior to this expanded melanophore. One to three small melanophores are present posterior to the anal base in most specimens 3.3-6.2 mm; none are present at 6.9-10.2 mm, and at >10.2 mm three or four melanophores are present here. A small, faint pigment spot is present in the midlateral line above the melanophore at the posterior end of the anal base in some specimens 3.1-5.5 mm, often connected to

TABLE 8.—Fin element counts in larval and juvenile *Stellifer lanceolatus*. Specimens between dashed lines are undergoing notochord flexion. Lengths are NL above upper dashed line, SL below.

NL or SL (mm)	Spinous dorsal	Soft dorsal	Anal	Pectoral[1]	Pelvic[1]	Caudal principal	Caudal procurrent
2.8	–	–	–	+	–	–	–
2.9	–	–	–	+	–	–	–
3.1	–	–	–	+	–	–	–
3.1	–	–	–	+	–	2+2	–
3.5	–	–	–	+	–	–	–
3.3	–	15	8	+	–	6+6	–
3.4	–	19	7	+	–	4+5	–
3.8	–	18	8	+	–	8+7	–
4.1	–	17	I,8	+	–	8+7	–
4.3	–	19	8	+	–	8+6	–
4.5	II	21	II,8	+	–	9+8	–
4.9	–	20	I,8	+	+	9+7	–
5.1	V	19	II,8	+	–	9+8	1,1
5.5	–	19	I,8	+	–	8+7	–
5.5	–	22	II,9	+	–	9+8	1,1
5.8	–	22	II,8	+	–	9+8	–
6.2	VII	22	II,8	+	+	9+8	2,2
6.9	XI	I,22	II,8	7	I,4	9+8	4,3
7.4	XI	I,23	II,8	13	I,5	9+8	4,4
7.6	XI	I,22	II,8	7	I,3	9+8	5,4
7.8	XI	22	II,8	13	I,5	9+8	6,4
10.2	XI	I,23	II,8	19	I,5	9+8	3,8
13.1	XI	I,22	II,8	19	I,5	9+8	9,8
13.9	XI	I,22	II,8	15	I,5	9+8	9,8
14.0	XI	I,23	II,8	19	I,5	9+8	9,8
15.1	XI	I,21	II,8	20	I,5	9+8	9,8

[1] + fin present, no developed elements.

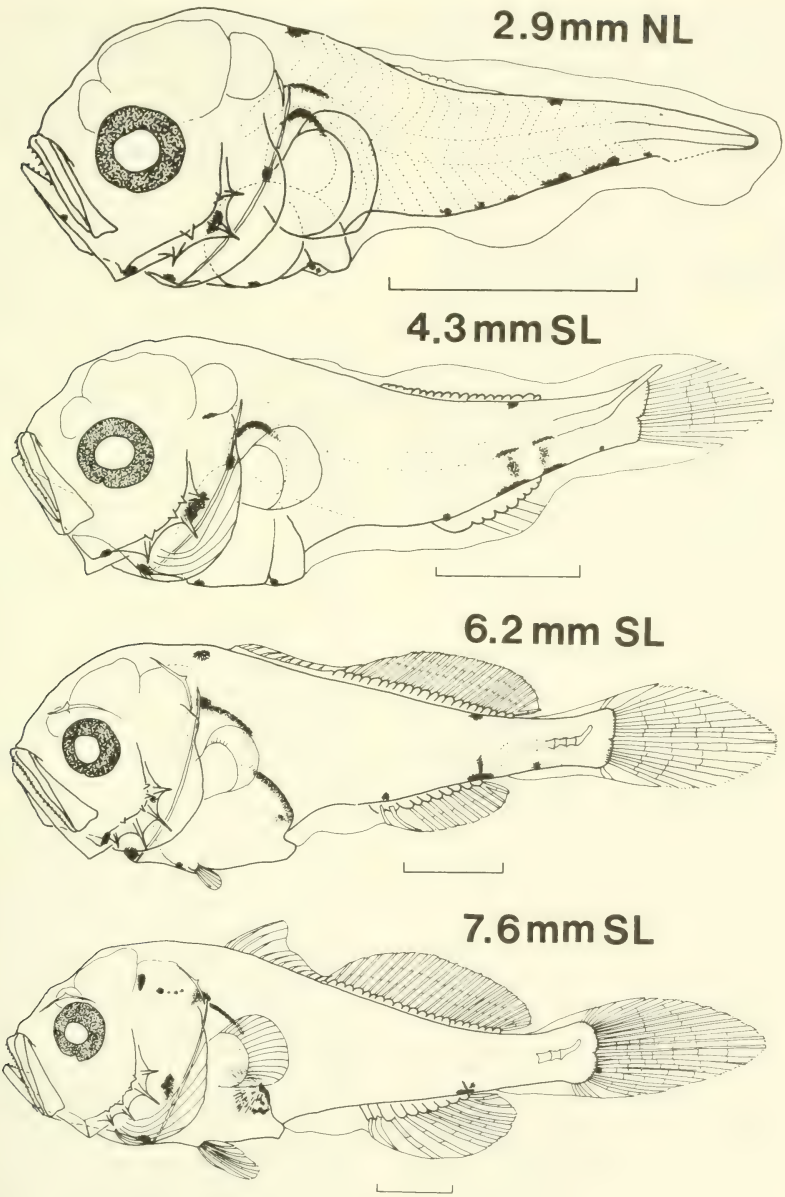


FIGURE 5.—Larval *Stellifer lanceolatus*. Scale equals 1 mm.

the dorsal branches of the expanded melanophore. A melanophore is present in the dorsal midline dorsal to the melanophore at the anal fin termination in most specimens 2.9-6.2 mm.

Head and visceral mass pigment is also useful in identifying larval *S. lanceolatus*. A large melanophore is present on the anterior surface of the visceral mass, between the cleithra, throughout development. A similar melanophore appears on the posterior surface of the visceral mass at ≥4.1 mm; this melanophore becomes extensively branched at ≥6.9 mm, and additional expanded melanophores appear dorsal and ventral to this one at ≥10.2 mm. In the ventral midline of the visceral mass a melanophore is present midway from cleithral symphysis to anus at 2.9-6.2 mm (between pelvic fin bases when present), and a second melanophore occurs on the anteroventral surface of the anus at 2.9-5.8 mm. In small larvae (≤3.8 mm), pigment is present in the dorsal midline and internally, on both sides of the notochord, above the visceral mass. A characteristic pigment area at the dorsal end of the operculum, which appears to roof a cavity in this area, is present at ≥7.4 mm. Pigment occurs at the angle of the lower jaw at <6.2 mm and anterior to the cleithral symphysis throughout the development.

Further pigment develops in late larvae (>10.2 mm). On the body surface, this includes a scattering of melanophores between the spinous dorsal and the visceral mass, four clusters of small melanophores in the dorsal midline along the dorsal fin base, and a few internal melanophores in the midlateral line above the anal base. Small melanophores appear in the spinous dorsal membrane and at the tip of the caudal fin at 13.1 mm, and in the soft dorsal membrane at 15.1 mm. Even in late larvae, pigmentation is not particularly heavy.

Identification of the series. The series was identified as *S. lanceolatus* by fin ray counts, pigmentation, caudal fin shape, and similarity to a published description of late larvae and juveniles. Fin ray counts of late larvae in this series (dorsal 21-23, anal 8) could be those of *B. chrysoura, M. americanus, M. saxatilis,* or *S. lanceolatus* (Table 1). Lack of heavy extensive body pigment indicates that the series is not *Menticirrhus*. The late larvae of the series have a lanceolate caudal fin, characteristic of *S. lanceolatus* but not of *B. chrysoura* (Hildebrand and Schroeder 1928; Dalhlberg 1975). Late larvae (≥9 mm) and early juveniles of *S. lanceolatus* described by Hildebrand and Cable (1934) represent a coherent series leading to a correctly identified young adult; late larvae of the series described here are similar to the late larvae of Hildebrand and Cable (1934), notably in the presence of an area of pigment at the upper end of the operculum, which appears to roof a cavity in this area.

Spawning season and area. Larval *S. lanceolatus* occurred in two South Carolina estuary samples in June and in one in July 1974; all three samples came from bottom rather than surface tows. Tidal pass sampling yielded five samples containing larvae in June and five with larvae in July; no larvae were taken from February to May. No *S. lanceolatus* larvae were taken in continental shelf tows. Thus, spawning appears to occur in estuarine and coastal waters, and not in shelf waters. Spawning occurs in early summer and may continue later into the year.

DISCUSSION

Comparisons with earlier descriptions

Bairdiella chrysoura

My material is in agreement with the description of Kuntz (1915), except that fin development occurs at larger sizes in Kuntz's description than in my material, and some pigment details are different. Kuntz's 5 mm specimen had a flexing notochord, 13 caudal rays, a developing dorsal fin base, and no anal base; these characters are found in my larvae of 4.3-4.4 mm. His 7.5 mm specimen is equivalent to my specimens of about 5.0 mm, having about 25 dorsal fin elements, 11 anal elements, no pelvic fin buds, and the full complement of caudal rays. Kuntz's larvae of ≤7.5 mm had a melanophore in the dorsal midline above the large melanophore of the ventral midline, present in only a few specimens ≤3.5 mm SL in my series, and a melanophore anterior to the dorsal fin origin, present in none of my specimens. These discrepancies may be due to Kuntz's use of fresh material while I used formaldehyde-preserved material. Shrinkage of formaldehyde-preserved larvae could account for the developmental differences, and melanophores may be contracted during preservation or degraded with storage in formaldehyde. Kuntz probably used total lengths rather than standard lengths which might par-

tially account for development rate discrepancies.

Jannke (see footnote 6) illustrated 2.0 mm and 5.0 mm larvae identified as *B. chrysoura*. The 2.0 mm specimen, smaller than my smallest larva, does not resemble Kuntz's larvae at similar sizes nor my earliest specimen in pigmentation. Jannke's 5.0 mm specimen is probably correctly identified: it has the fin counts and the characteristic cleithral pigment swath of *B. chrysoura* but lacks characteristic pigment of the ventral midline.

Larimus fasciatus

My material agrees fairly well with the only published description, that of Hildebrand and Cable (1934). The pigmented pectoral fin, emphasized by Hildebrand and Cable (1934), would appear to confirm identification of all specimens of their series. The drawings are not in good agreement with the description in their text; for example, their drawing of a 4.5 mm specimen shows none of the pigment described. The pigment of the brain which I have found characteristic of *L. fasciatus* larvae was not mentioned by Hildebrand and Cable; perhaps fading due to preservation was responsible. The few body proportions given by Hildebrand and Cable (particularly the position of the anus at >50% SL) are characteristic of *L. fasciatus*.

Stellifer lanceolatus

Hildebrand and Cable's (1934) description of a series identified as *S. lanceolatus* was based on a mixture of that species and *L. fasciatus*. Early larvae (≤3.5 mm SL) had pigmented pectoral fins and developing pectoral rays characteristic of *L. fasciatus*. Later larvae (≥4.5 mm SL) lacked pectoral fin and brain pigment and showed pectoral ray development only at >5.6 mm. Body depth and preanus length values of the early larvae are closer to those of *L. fasciatus* than of *S. lanceolatus*. Characters given by Hildebrand and Cable (1934) for separating early *L. fasciatus* and *S. lanceolatus* were preopercular spination, mouth shape, maxillary length, and amount of space around the brain. However, my observations indicate that none of these characteristics are suitable for separating these species.

As with *L. fasciatus*, there are discrepancies between text and illustrations in the description of Hildebrand and Cable (1934), particularly in the early stages. My material agrees fairly well with that of Hildebrand and Cable (1934) at ≥4.5 mm SL, although I observed a dorsal midline melanophore dorsal to the termination of the anal fin in specimens ≤7.0 mm SL, which was not indicated by those authors.

Spawning Seasons and Areas

Bairdiella chrysoura

Spawning is reported by various authors to occur in late spring and summer on the east coast of the United States and the Gulf of Mexico, and year-round in South Florida. The season appears to begin later and to be shorter at higher latitudes: June to August off New Jersey (Welsh and Breder 1923), May to July in Delaware Bay (Thomas 1971) and Chesapeake Bay (Hildebrand and Schroeder 1928; Joseph et al. 1964), April to August at Beaufort, N.C. (Kuntz 1915), April to May off Georgia (Dahlberg 1972), and April to September off Louisiana (Sabins 1973). Year-round spawning with peaks in January to February and April to June is reported in South Florida (Jannke see footnote 6). Spawning occurs at least April to July in South Carolina waters, according to data presented in the present study.

Spawning reportedly occurs primarily in estuarine and coastal waters, and this is indicated by my data also. Hildebrand and Cable (1930) reported captures of eggs and early larvae in estuaries and to 19-24 km offshore off Beaufort, N.C., but the reliability of their identifications is uncertain. Their descriptions of eggs and early larvae of *B. chrysoura* are insufficiently detailed to ensure separation from those of other sciaenid and perciform fishes. Jannke (see footnote 6) and Sabins (1973) judged from the small size of larvae caught in tidal passes that spawning must have occurred nearby in estuarine or coastal waters. Specimens I examined were mostly taken in South Carolina estuaries and tidal passes, with only one specimen coming from continental shelf waters.

Larimus fasciatus

The information I have presented and the limited literature reports available indicate a long spawning period, extending at least from May to October, for *L. fasciatus*. Although larvae were more abundant in MARMAP tows made from August to September than tows made from April to May, larvae were abundant in NMFS Sandy Hook

Laboratory plankton tows made in May and in July. Hildebrand and Cable (1934) took specimens of length <5 mm from July to October off Beaufort, but presence of small juveniles in these months indicated spawning began in May. Larvae were taken from April to October in plankton tows between Chesapeake Bay and Cape Lookout, N.C. (Berrien et al. 1978).

Spawning apparently occurs in continental shelf waters. I obtained no larvae from South Carolina estuaries, but larvae were abundant in continental shelf plankton tows. Hildebrand and Cable (1934) took larvae from the coast to 22 km offshore. Larvae were common in plankton tows in continental shelf waters between Chesapeake Bay and Cape Lookout (Berrien et al. 1978).

Stellifer lanceolatus

My data point to spawning at least in June and July in South Carolina waters; later spawning may occur but no samples were available from the second half of the year. Hildebrand and Cable (1934) reported presence of small larvae from July to September, but their small "*S. lanceolatus*" were probably *L. fasciatus* so this report may not be accurate. Welsh and Breder (1923) reported spawning in late spring and early summer on the U.S. east coast, and Dahlberg (1972) reported May to September spawning off Georgia. Fahay (1975) reported a 28.2 mm SL specimen taken in October off Florida.

Spawning in coastal and estuarine waters rather than continental shelf waters was indicated by my observations. Hildebrand and Cable (1934) reported small larvae from the coast to 22 km offshore, but again these larvae may have been misidentified. Larvae have been taken in Georgia estuaries (Berrien[8]). Fahay's (1975) single specimen was from inshore 7.5 km south of Cape Canaveral; being relatively large, this specimen could have originated in another spawning area.

Comparisons With Other Larval Sciaenidae

Larimus fasciatus

Although superficially similar to larvae of several other marine sciaenids, of the southeast United States, *L. fasciatus* larvae are easily separated from all others by pigmentation, fin development sequence, and preanus distance. Forebrain pigment and pectoral fin pigment are not present in early larvae (larvae with dorsal and anal fin rays undeveloped or incompletely developed) of other sciaenids of the area, and pigment on the anterior surface of the midbrain appears earlier than in other sciaenids of the area. Pectoral fin rays begin development earlier than in other sciaenids of the area, in fact earlier than in larvae of most known teleosts. The preanus distance of >50% SL is greater than in other sciaenid larvae of the area.

Bairdiella chrysoura and *Stellifer lanceolatus*

These species are treated together because they are quite similar as larvae, and resemble larvae of other species, notably *Cynoscion regalis* (Pearson 1941) and *Cynoscion nothus* (Stender[9]). Typical larvae of *B. chrysoura* have a well-developed swath of pigment from nape to cleithral symphysis, which is not found in larvae of the other species; however, melanophores of the swath may be contracted or faded by preservation. Pigment of the ventral midline posterior to the anus is the most reliable character for separation of *B. chrysoura* from *S. lanceolatus* larvae. Both have a melanophore at the posterior end of the anal fin base; however, *B. chrysoura* has a melanophore anterior to the anal fin base (at 4.1-7.0 mm SL) and a melanophore at the anterior end of the anal base, while *S. lanceolatus* has no melanophore anterior to the anal base but has a melanophore just posterior to the anterior end of the anal base (at the base of the second anal spine when this is developed).

Larvae of the two *Cynoscion* species mentioned can be separated from larval *B. chrysoura* and *S. lanceolatus* by careful attention to pigment of the midventral line (Stender see footnote 9; pers. observ.). Identification of small larvae with undeveloped anal fin bases may be difficult, since the characteristic pigment sequences develop (from a row of small melanophores) at about the same time as anal-base development. Presence of a melanophore in the dorsal midline, above the posterior end of the anal base, in most *S. lan-*

[8]Peter L. Berrien, Fishery Biologist, Northeast Fisheries Center Sandy Hook Laboratory, National Marine Fisheries Service, NOAA, Highlands, NJ 07732, pers. commun. May 1975.

[9]Bruce W. Stender, Biologist, South Carolina Wildlife and Marine Resource Division, P.O. Box 12559, Charleston, SC 29412, pers. commun. February 1978.

ceolatus 2.9-6.9 mm SL may also assist in separating the species; such a melanophore is present in only a few *B. chrysoura* at ≤3.5 mm SL.

Cynoscion regalis has a single melanophore in the dorsal midline above the anal fin throughout development.

ACKNOWLEDGMENTS

I am grateful to Malcolm H. Shealy, Jr., South Carolina Estuarine Survey Program, Charles Farmer and Charles Boardman, South Carolina Crustacean Management Program, and Ronald Hodson, North Carolina State University, for permission to use sciaenid specimens from their collections, and to Peter L. Berrien, Northeast Fisheries Center Sandy Hook Laboratory, for data on *Larimus fasciatus* collections off the southeastern United States. Bruce W. Stender has been a stimulating collaborator on studies of larval sciaenids and carefully reviewed the manuscript. Paul A. Sandifer, Charles A. Barans, and Peter Berrien also reviewed the manuscript. Hope Mixson sorted larvae from samples. Kathleen Meuli and Lyne Imbeau typed the manuscript. To all many thanks. This research was supported by the National Marine Fisheries Service MARMAP (Marine Resources Monitoring, Assessment and Prediction) Program under contract number 6-35147.

LITERATURE CITED

ANDERSON, W. W.
1968. Fishes taken during shrimp trawling along the South Atlantic Coast of the United States, 1931-35. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 570, 60 p.

BAILEY, R. M., J. E. FITCH, E. S. HERALD, E. A. LACHNER, C. C. LINDSEY, C. R. ROBINS, AND W. B. SCOTT.
1970. A list of common and scientific names of fishes from the United States and Canada. 3d ed. Am. Fish. Soc. Spec. Publ. 6, 149 p.

BERRIEN, P. L., M. P. FAHAY, A. W. KENDALL, JR., AND W. G. SMITH.
1978. Ichthyoplankton from the RV *Dolphin* survey of continental shelf waters between Martha's Vineyard, Massachusetts and Cape Lookout, North Carolina, 1965-66. U.S. Dep. Commer., NOAA, Sandy Hook Lab. Tech. Serv. Rep. 15, 152 p.

CHAO, L. N.
1978. A basis for classifying western Atlantic Sciaenidae (Teleostei: Perciformes). U.S. Dep. Commer., NOAA Tech. Rep. NMFS Circ 415, 64 p.

CLARK, J., W. G. SMITH, A. W. KENDALL, JR., AND M. P. FAHAY.
1969. Studies of estuarine dependence of Atlantic coastal fishes. Data Report I: Northern section, Cape Cod to Cape Lookout. R.V. *Dolphin* cruises 1965-66: Zooplankton volumes, mid-water trawl collections, temperatures and salinities. U.S. Fish Wildl. Serv. Tech. Pap. 28, 132 p.
1970. Studies of estuarine dependence of Atlantic coastal fishes. Data Report II: Southern section, New River Inlet, N.C., to Palm Beach, Fla. R.V. *Dolphin* cruises 1967-68: Zooplankton volumes, surface-meter net collections, temperatures, and salinities. U.S. Bur. Sport Fish. Wildl. Tech. Pap. 59, 97 p.

DAHLBERG, M. D.
1972. An ecological study of Georgia coastal fishes. Fish. Bull, U.S. 70:323-353.
1975. Guide to coastal fishes of Georgia and nearby states. Univ. Ga. Press, Athens, 186 p.

FAHAY, M. P.
1975. An annoted list of larval and juvenile fishes captured with surface-towed meter net in the South Atlantic Bight during four RV *Dolphin* cruises between May 1967 and February 1968. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-685, 39 p.

GINSBURG, I.
1929. Review of the weakfishes (*Cynoscion*) of the Atlantic and Gulf coasts of the United States, with a description of a new species. Bull. U.S. Bur. Fish. 45:71-85.

HILDEBRAND, S. F., AND L. E. CABLE.
1930. Development and life history of fourteen teleostean fishes at Beaufort, N.C. Bull. U.S. Bur. Fish. 46:383-488.
1934. Reproduction and development of whitings or kingfishes, drums, spot, croaker, and weakfishes or sea trouts, family Sciaenidae, of the Atlantic coast of the United States. U.S. Bur. Fish, Bull. 48:41-117.

HILDEBRAND, S. F., AND W. C. SCHROEDER.
1928. Fishes of Chesapeake Bay. Bull. U.S. Bur. Fish. 43 (part 1), 388 p.

HOESE, H. D., AND R. H. MOORE.
1977. Fishes of the Gulf of Mexico, Texas, Louisiana, and adjacent waters. Texas A&M Univ. Press, College Station, 327 p.

JOHNSON, G. D.
1978. Development of fishes of the mid-Atlantic Bight, an atlas of egg, larval and juvenile stages, Volume IV. Carangidae through Ephippidae. U.S. Dep. Inter., Fish Wildl. Serv., Biol. Serv. Program, FWS/OBS-78/12, 314 p.

JORDAN, D. S., AND B. W. EVERMANN.
1896. The fishes of north and middle America: a descriptive catalogue of the species of fish-like vertebrates found in the waters of North America, north of the Isthmus of Panama. U.S. Natl. Mus. Bull. 47, 3313 p. (4 vols.)

JOSEPH, E. B., W. H. MASSMANN, AND J. J. NORCROSS.
1964. The pelagic eggs and early larval stages of the black drum from Chesapeake Bay. Copeia 1964:425-434.

KEISER, R. K., JR.
1976. Species composition, magnitude and utilization of the incidental catch of the South Carolina shrimp fishery. S.C. Mar. Resour. Cent. Tech. Rep. 16, 95 p.

KUNTZ, A.
1915. The embryology and larval development of *Bairdiella chrysura* and *Anchovia mitchilli*. Bull. U.S. Bur. Fish. 33:1-19.

MILLER, G. L., AND S. C. JORGENSON.
1973. Meristic characters of some marine fishes of the Western Atlantic Ocean. Fish. Bull., U.S. 71:301-312.

PEARSON, J. C.
1929. Natural history and conservation of redfish and

other commercial sciaenids on the Texas coast. Bull. U.S. Bur. Fish. 44:129-214 (Doc. 1046).

1941. The young of some marine fishes taken in lower Chesapeake Bay, Virginia, with special reference to the gray sea trout *Cynoscion regalis* (Bloch). U.S. Fish Wildl. Serv., Fish. Bull. 50:79-102.

POWLES, H., AND B. W. STENDER.

1978. Taxonomic data on the early life history stages of Sciaenidae of the South Atlantic Bight of the United States. S.C. Mar. Resour. Cent. Tech. Rep. 31, 64 p.

RANDALL, J. E.

1968. Caribbean reef fishes. T.F.H. Publications Inc., Hong Kong, 318 p.

SABINS, D. S.

1973. Diel studies of larval and juvenile fishes of the Caminada Pass area, Louisiana. M.S. Thesis, Louisiana State Univ., Baton Rouge, 163 p.

SCOTTON, L. N., R. E. SMITH, N. S. SMITH, K. S. PRICE, AND D. P. DE SYLVA.

1973. Pictoral guide to fish larvae of Delaware Bay. Del. Bay. Rep. Ser. Coll. Mar. Stud. Univ. Del. 7, 206 p.

SHEALY, M. H., JR., J. V. MIGLARESE, AND E. B. JOSEPH.

1974. Bottom fishes of South Carolina estuaries — relative abundance, seasonal distribution, and length-frequency relationships. S.C. Mar. Resour. Cent. Tech. Rep. Ser. 6, 189 p.

THOMAS, D. L.

1971. An ecological study of the Delaware River in the vicinity of Artificial Island. Part III. Six species of drum (Sciaenidae) in the lower Delaware River, a brackish tidal estuary. Ichthyol. Assoc. Bull. 3:1-247.

WELSH, W. W., AND C. M. BREDER, JR.

1923. Contributions to life histories of Sciaenidae of the eastern United States coast. Bull. U.S. Bur. Fish. 39:141-201.

REPRODUCTIVE BIOLOGY OF THE VERMILION SNAPPER, *RHOMBOPLITES AURORUBENS*, FROM NORTH CAROLINA AND SOUTH CAROLINA

CHURCHILL B. GRIMES[1] AND GENE R. HUNTSMAN[2]

ABSTRACT

The vermilion snapper, *Rhomboplites aurorubens*, a species often associated with Caribbean reefs and banks, is an important recreational fish of the outer continental shelf of North Carolina and South Carolina. Serial spawning occurs from late April through September off the Carolinas at depths ranging from 31 to 91 m. Most females spawn in the third or fourth year at about 205-275 mm total length. Larger, older females (age 5-10; up to 530 mm total length) appear to spawn longer each reproductive season, which may be an optimal strategy for maximizing reproductive biomass (balancing the physiological costs of somatic and gonadal growth).

Overall sex ratio is unequal in favor of females (approximately 60%), but the ratio is 1:1 for small fish (less than 150 mm total length) and heavily in favor of large females (69-100% for fish greater than 500 mm total length) because they live longer than males. Fecundity of first spawners is estimated at 17-42 thousand eggs, and large females produce 1.5 million eggs.

The vermilion snapper, *Rhomboplites aurorubens*, is a small lutjanid which grows to 600 mm total length (TL) and 2,600 g (illustrated in Böhlke and Chaplin 1968). It occurs from Cape Hatteras, N.C., to Bermuda, southward throughout the Gulf of Mexico and Caribbean Sea to southeastern Brazil. The species is abundant, ranking second or third in weight and numbers in the Carolina headboat[3] fishery (which landed between 590 and 730 metric tons of demersal fishes annually) between 1972 and 1975 (Huntsman 1976).

Vermilion snapper and other reef fishes normally associated with deep (>70-90 m) Caribbean reefs and banks occur in two habitats of the outer continental shelf of the Carolinas (Figure 1). The most spectacular of the habitats, the shelf break zone (Struhsaker 1969), occurs at the edge of the continental shelf (55-180 m) where the gently sloping bottom plunges abruptly downward as the continental slope. It is an area of jagged peaks, precipitous cliffs and rocky ledges associated with drowned Pleistocene reefs (MacIntyre and Milliman 1970). The second habitat (inshore live bottom) occurs at 25-55 m and consists of broken reefs and rock outcroppings, rocky ledges, and coral patches dispersed over the continental shelf shoreward of the shelf break zone.

Knowledge concerning reproduction of the vermilion snapper is lacking. Longley and Hildebrand (1941) reported gravid specimens about the Tortugas, Fla., in July and concluded that spawning takes place in midsummer. Breder (1929) wrote that vermilion snapper probably spawn in early spring along the South Atlantic coast of the United States, and Walker (1950) reported spawning off North Carolina in February. Monroe et al. (1973) collected a ripe female off Jamaica in November, and Fahay (1975) and Laroche (1977) recorded larvae off Georgia in July and August. Erdman (1976) found ripe fish from February through June in the northeastern Caribbean.

In this paper we describe the seasonality, spawning frequency, sex ratio, age and size at maturity, and fecundity of the vermilion snapper and discuss possible adaptive strategies for its reproduction.

The study area (Cape Hatteras, N.C., to Charleston, S.C.) was stratified by depth (i.e., inshore and offshore, the dividing depth being 55 m), and specimens were collected throughout. Most fish were obtained from the recreational fisheries throughout the Carolinas; however, some specimens were collected by hook and line or trawl from

[1]Department of Environmental Resources, Cook College and New Jersey Agricultural Experiment Station, Rutgers University, New Brunswick, NJ 08903.

[2]Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 570, Beaufort, NC 28516.

[3]Headboats are recreational fishing vessels which charge anglers for a day's fishing on an individual, thus "per head," basis.

Manuscript accepted July 1979.
FISHERIES BULLETIN: VOL. 78, NO. 1, 1980.

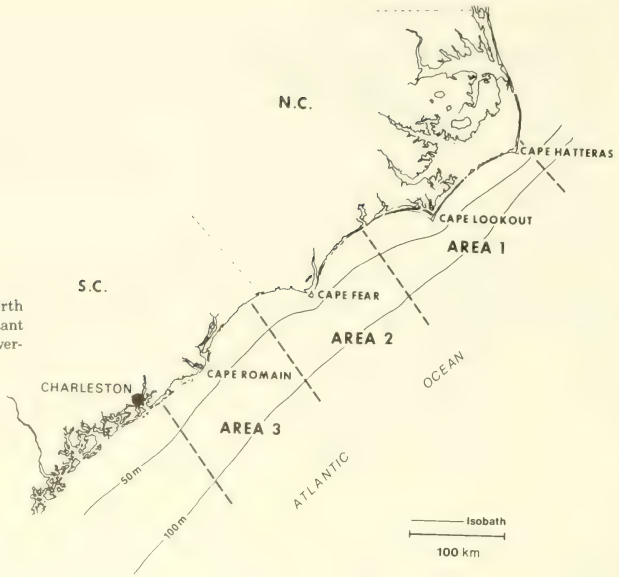


FIGURE 1.—Continental shelf off North Carolina and South Carolina and important bathymetric features that relate to the vermilion snapper study.

the RV *Onslow Bay* and the RV *Eastward*; most juveniles were trawled from RV *Dolphin*.

Temperature was taken by expendable bathythermograph, and photoperiod was obtained from the National Ocean Survey tide tables (U.S. Department of Commerce 1971, 1972, 1973). Specimens were weighed (nearest gram) and measured (nearest millimeter). Gonads were removed, preserved in 10% Formalin[4] for at least 1 wk, washed in tap water for several days, and then placed in 70% isopropyl alcohol. Frequency distributions of ovum diameters were plotted by month to determine seasonality, frequency, and duration of spawning (Hickling and Rutenberg 1936; Fahay 1954). The diameters of approximately 100 randomly selected ova from each of two females per month were measured to the nearest 0.05 mm by dissecting binocular microscope at 25×. To validate measuring ova from any portion of an ovary, we determined by analysis of variance that ova sizes were distributed uniformly (indicating uniform development) throughout the ovaries (Table 1).

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Later, the gonads were removed from preservative and weighed (nearest 0.1 g) after surface moisture was absorbed by blotting.

A gonosomatic index was used as a measure of reproductive development (Finkelstein 1969) for determining spawning seasonality and maturity. The index was calculated according to the formula $KG = W/TL^3$ where KG = gonad index, W = preserved (blotted dry) gonad weight in grams, TL = total length in millimeters. We realize that assuming the cubic relationship is arbitrary. Quast (1968) has shown for kelp bass, *Paralabrax clathratus*, that the percentage of body weight contained in gonads increases with fish length. Therefore, the true exponent is undoubtedly >3, but data limitations preclude more accurate formulation.

Ovaries used for fecundity studies were preserved in modified Gilson's fixative (Bagenal and Braum 1968). The ovarian tunic was removed and washed free of adhering ova. Additional washings separated developing ova from undifferentiated oöcytes and follicular material. A small subsample of ova (about 1,000 or less) was stored wet for later counting in a gridded Petri dish under a binocular dissecting scope. Subsamples and origi-

TABLE 1.—Analysis of variance testing the hypothesis that there is no difference in ovum diameters between anterior, posterior, and center sections of ovaries from three vermilion snapper. NS = not significant.

Fish no.	Source of variation	df	MS	F
1	Between sections	2	1.0769	0.46 NS
	Within sections	309	2.341	
2	Between sections	2	0.5417	0.97 NS
	Within sections	309	0.5770	
3	Between sections	2	29.907	1.09 NS
	Within sections	309	27.3512	

nal ova samples (total sample minus counting subsample) were drained and dried for 24 h at 40° C. Subsample and original ova sample dry weights were determined to 0.001 g on a beam balance, and the sum of these two weights provided the total ova sample dry weight. Fecundity was determined by proportionality where:

$$\frac{\text{fecundity}}{\text{total ova dry weight}} = \frac{\text{number of ova in subsample}}{\text{subsample dry weight}}.$$

Fecundity models were fitted by semilog transformation (log fecundity = $a + b \times$ length, weight, or age) and regressions are the functional regressions of Ricker (1973). The semilog formulation of fecundity models was used instead of more traditional log-log models because they fit the data best.

RESULTS

Seasonality, Frequency, and Duration of Spawning

Several lines of evidence indicate that spawning occurs from late spring through early fall. Males and females with ripe-appearing gonads were collected from late April through September, but few females were collected with ova loose within the ovarian tunic. Microscopic examination of preserved ovaries showed three types of maturing ova present during this period (in addition to maturing ova, undifferentiated transparent oöcytes were present and were by far the most numerous): the smallest developing ova (0.11-0.2 mm in diameter) were translucent and were the most numerous developing type; the next largest ova (0.33-0.43 mm in diameter) were nearly opaque throughout and less abundant than the preceding; the largest developing ova (0.46-0.71 mm in diameter) were typical mature teleost eggs with opaque cytoplasm occupying one pole of the egg which also contained transparent to translucent yolk material and oil globules. We observed these most mature ova only in ovaries collected from May to September, although what appeared to be ripe ovaries were also seen in April; furthermore, these mature ova occurred in only 7 of 149 ripe-appearing ovaries examined.

Frequency distributions of maturing ovum diameters (Table 2) show at least two size modes of ova present from April to October (three were present in one of two June samples), while only one smaller size mode or undifferentiated oöcytes were present in November, December, and March. No ova collected in January or February were examined. These data indicate spawning begins in late April or May and continues through September or perhaps early October.

Monthly mean gonad index values for 101 sexually mature females, sampled from May 1972 to April 1974, also denote late spring to fall spawning (Figure 2). No fish were collected in January or February 1973 or 1974; however, adult females collected in February 1975 had gonad index values of 0.51 and 0.40 which are consistent with gonad index trends indicated in Figure 2. Increasing

TABLE 2.—Developing ovum diameter-frequency distributions (percent) from two female vermilion snapper that were examined during various months of the study.

0.08 mm interval (midpoint)	1972 May	June	July	Aug.	Sept.	Oct.	Nov.	1973 Mar.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	1974 Apr.
0.06				1													
0.14	40	45	39	29	35				35	16	17	28	19	80	100		26
0.22	27	13	32	15	8				21	49	22	36	38	12			17
0.30	11	7	7	2	1				10	5	5	11	16				14
0.38	11	10	6	9	12				5	9	17	10	13	6			13
0.46	4	25	2	8	41				28	15	36	9	13	2			27
0.54	4		1	13	3				1		3	6	1				3
0.62	3		5	23								2					
0.70			8							4							
0.78										2							
Total	194	198	172	214	227				179	199	209	200	197	100	100		200
Mean, mm	0.25	0.27	0.27	0.37	0.32	—	—	—	0.28	0.29	0.34	0.27	0.27	0.17	0.14	—	0.3

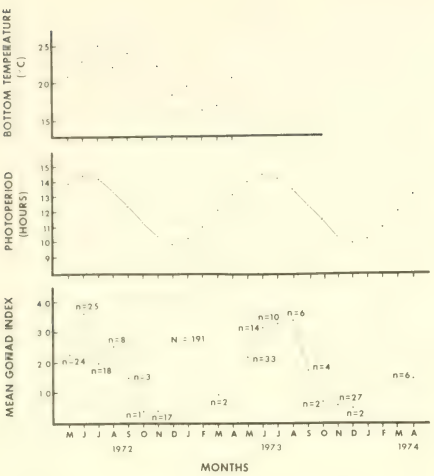


FIGURE 2.—Monthly mean gonad index of female vermilion snapper collected from May 1972 to April 1974, mean bottom temperatures at collecting sites, and photoperiod (U.S. Department of Commerce 1971, 1972, 1973).

monthly mean gonad index is well correlated with lengthening photoperiod and increasing bottom temperature.

The seasonal occurrence of juveniles and the large size variation within the youngest age-group provides additional evidence of an extended summer spawning season. During October and November 1973, several hundred juveniles ranging from 53 to 227 mm TL were trawled in Long Bay, N.C. and S.C., and also off Charleston. Aging of these fish from scales showed the sample to contain mostly age-groups 0 and 1. Using the growth rate for the first year of life (Grimes 1978) for extrapolating backwards, we determined that the age 0 fish collected in October and November 1973 were spawned throughout the summer months.

Although actual spawning was never observed, it probably occurs around rough bottom from 31 to 91 m but may be more concentrated in deeper areas (55-91 m). Ripe fish were taken over rough bottom at depths of 31-91 m when bottom temperatures were 20.6°-24.8° C. In Raleigh Bay and northern Onslow Bay, ripe fish were more abundant from 55 to 91 m; however, in the southern portion of the study area (southern Onslow Bay and Long Bay) ripe individuals were more equally distributed with depth.

Reproductive synchrony within schools may be indicated by hook-and-line sampling. Fish were usually caught in sudden bursts of fishing activity; seldom were single individuals encountered. Gonad indices for fish of similar size caught over a short time interval (probably from the same school) were nearly identical, indicating that reproduction within schools may be highly synchronized.

Multiple spawnings each season are indicated by the relative abundance of ova types (described earlier) at different times during the spawning season (Table 2). Maturing ova were present April through October and spawning apparently takes place during this period. Early in the spawning season (May) all three developing ova types were present in considerable abundance. When ripe ova were present later in the season (June or July), fewer smaller developing ova occurred. In August and September (late in the spawning season) when ripe ova were present, smaller developing ova were absent. The total of the developing ova types may represent all that will be spawned that season, and at each spawning a female develops only as many ova as her abdominal capacity will allow. This process could be repeated a number of times during the season until all eggs are spawned.

Variation in gonad index during the spawning period for similar size fish may also indicate fractional spawning. This was evident during the spawning months of 1972 and 1973 when the gonad index of both males and females of similar size varied by as much as a factor of 12 (Figure 3). The small size of ripe gonads combined with high fecundity (see subsequent discussion) is additional evidence for fractional spawning. The mean percent of body weight (observed) for ovaries of mature females collected during spawning months was 2.4% (0.6-5.8%, n = 40). Mature males had testes averaging 1.1% of body weight (0.4-2.4%, n = 15) during the same months. Also, we frequently observed semiflacid ovaries with no loose ova (perhaps partially spawned) in large adult females from June through September.

Maturation

Age and growth data of Grimes (1978) and our reproductive data indicate that most fish attain sexual maturity during their third or fourth years of life (186-256 and 256-324 mm TL), but a few

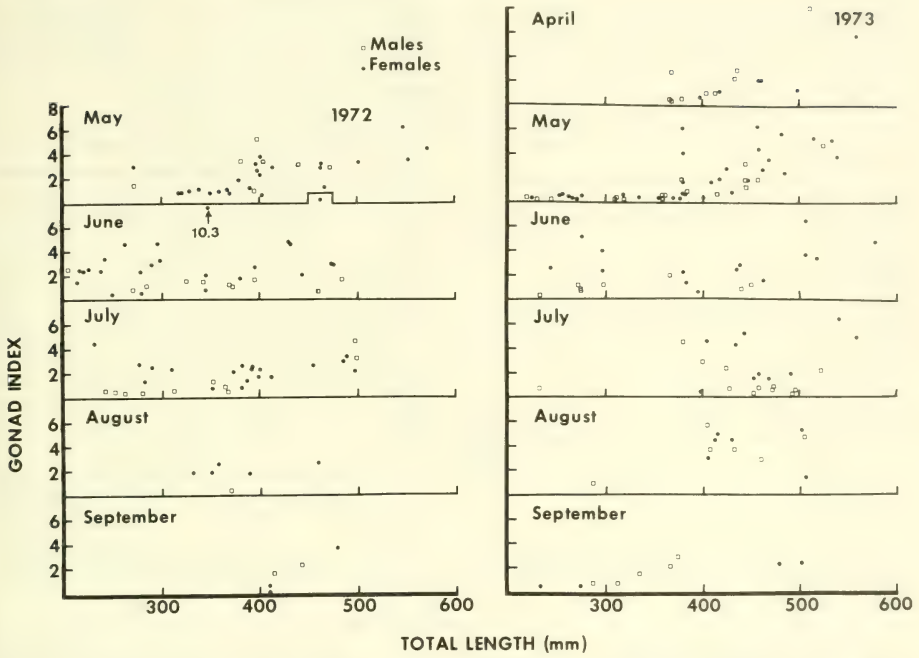


FIGURE 3.—Individual gonad index (gonad weight/(total length)^3) values for vermilion snapper over the spawning months of 1972 and 1973 plotted against total length.

precocious individuals may mature in their second year (100-186 mm TL) at about 150 mm TL. We determined age and size at maturity by examining a plot of monthly mean gonad index of females collected in the spawning season (June-September) by total length (Figure 4). Furthermore, spawning season (April-September) gonad index values for males and females (Figure 3) and monthly mean gonad index for each age-group of fish (Figure 5) show that fish age 4-9 (>324 mm TL) ripen earlier (April or May vs. June) and remained in reproductive condition longer (April to September vs. June to August) than younger spawning fish.

Sex Ratio

Sex ratio varies significantly from 1:1. From 1972 to 1974 we sexed 874 fish; 546 (62.5%) were females and 328 (37.5%) were males (1 df; $\chi^2 = 54.4$; $P<0.001$). The total sample was analyzed by

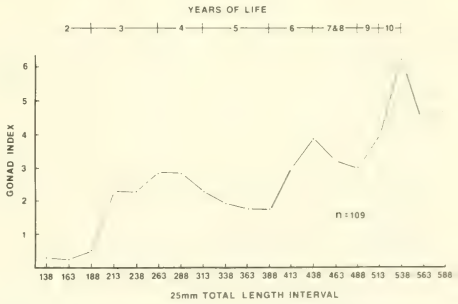


FIGURE 4.—Mean gonad index plotted by 25 mm TL intervals for female vermilion snapper during the spawning season (June-August). Approximate size at age was determined from Grimes (1978).

year of collection and sex ratios were judged significantly different from 1:1 in all years (Table 3). Higher proportions of females (62.5%) were col-

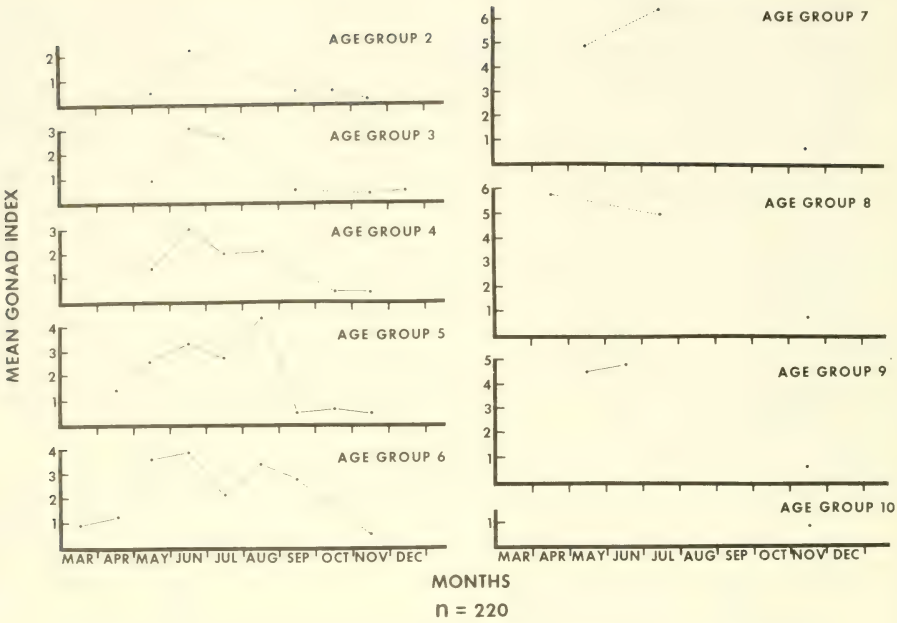


FIGURE 5.—Monthly mean gonad index (gonad weight / (total length)^3) for female vermilion snapper by age-group.

TABLE 3.—Test of the hypothesis that sex ratios of vermilion snapper did not vary significantly from 1:1 within years of collection.

Item	1972	1973	1974
Percentage of females	71.9	59.4	62.5
Sample size	135	424	315
Chi-square value	25.8*	15.1*	20.8*

*$P < 0.01$.

TABLE 4.—Tests of the hypothesis that sex ratio of vermilion snapper did not vary significantly from 1:1 within 50 mm TL intervals.

Total length (mm)	n	Females (%)	Chi-square	Total length (mm)	n	Females (%)	Chi-square
101-150	105	49.5	0.0096	401-450	102	63.8	7.19*
151-200	117	63.4	8.83*	451-500	60	61.7	3.27
201-250	68	49.3	0.014	501-550	58	69.2	7.69*
251-300	99	61.2	4.94*	551-600	32	89.3	17.28*
301-350	90	59.4	3.38	601-650	1	100	
351-400	142	65.9	12.7*				

*$P < 0.05$.

lected at shelf break habitats than inshore live bottom (60.5%), but the hypothesis that sex ratio and capture depth were independent was not rejected (χ^2 $P > 0.05$, $n = 852$).

There is a significant difference in sex ratio throughout the life of the fish (as estimated by total length); however, differences within some size intervals were not judged significant (Table 4). Contingency-table analysis showed that sex ratio and size were dependent (χ^2 $P > 0.05$, df = 9) (i.e., with growth sex ratios were different from 1:1 and changed significantly). In small fish (101-150 mm TL) the number of males and females was nearly equal, but at 151-200 mm TL the percentage of females increased to about 60%, where it remained somewhat stable until 501-550 mm TL, when percentage of females began to steadily increase (Table 4). Only one fish >600 mm TL was collected (618 mm) and it was a female.

Fecundity

Estimates of fecundity ranged from 8,168 to 1,789,998 ova for 41 females ranging from 229 to 557 mm TL (3-8 yr old and 136-2,293 g). Because

females may spawn several times per season, fecundity estimates were from ovaries collected early in the spawning season (May and June) and all classes of maturing ova were counted.

In Table 5, fecundity was separately regressed on total length (millimeters), weight (grams), and age (years) and, as expected, fecundity increases as a function of all three correlates. Fecundity increases so markedly in larger (older) fish (Figure 6) that semilog models were needed to adequately describe the relationship between fecundity and length, weight, and age. Length and weight are approximately equally good predictors of fecundity (r = 0.864 and 0.863, respectively). First spawners probably are about 205-275 mm TL and produce between 16,800 and 41,700 eggs. This estimate assumes that spawning extends from late June through September for young fish (age 2-4), that first spawning occurs in the third or fourth year (186-256 or 256-324 mm TL), that scale annuli form in March (Grimes 1978), and that approximately 25% of annual growth occurs from annulus formation to late June.

TABLE 5.—Functional equations for fecundity in vermilion snapper. Age (A) determined from scales.

Predictor	Equation	r	n
Total length (mm)	$F = \exp(7.07 + 0.013TL)$	0.863	41
Age (yr)	$F = \exp(7.57 + 0.873A)$	0.853	41
Weight (g)	$F = \exp(10.21 + 0.002W)$	0.864	41

FIGURE 6.—The relationship of fecundity to total length of female vermilion snapper.

DISCUSSION

Spawning Seasonality

The conclusion that spawning occurs from late April through September is corroborated by Longley and Hildebrand's (1941) statement that spawning took place in summer around the Tortugas. Powles[5] and Fahay (1975) reported that larvae were collected at the surface off South Carolina and Georgia in June and July, and Laroche (1977) described a larval series collected off Georgia in August. Walker (1950), however, reports collecting vermilion snapper in spawning condition off North Carolina in February. Erdman (1976) sampled 400 vermilion snapper in the northeastern Caribbean and found fish in spawning condition January through June. Monroe et al. (1973) collected a ripe female in November off Jamaica and suggested, on the basis of these and more extensive data for other reef species, that spawning probably occurs year-round in the Caribbean, but that peak spawning is in winter where surface temperature is about 26.5° C. The larvae reported on by Fahay (1975) and Laroche (1977) were collected at 27° and 26.5° C, respectively, and we collected ripe fish off North Carolina when sea surface temperature was between 26° and 27° C.

It appears that spawning of vermilion snapper off North Carolina and South Carolina is restricted to warm months (late April or May-September), yet spawning may occur almost year-round in the Caribbean (Monroe et al. 1973; Erdman 1976). Similar life history variations in response to local environmental conditions are reported by Leggett and Carscadden (1978) for American shad.

[5]H. Powles, Fishery Biologist, South Carolina Marine Resource Center, Charleston, S.C., pers. commun. May 1975.

Several authors report fractional spawning in marine fishes (Starck and Schroeder 1971; Beaumarriage 1973; de Silva 1973; Macer 1974). Our inference that variation in gonad index during a spawning month for similar size fish suggests fractional spawning is supported by Starck and Schroeder's (1971) findings on a related species, *Lutjanus griseus*, the gray snapper. They concluded, from variation of ovary lengths and weights from fish of similar size, that spawning probably occurs more than once in the same season in south Florida waters.

In the results, we described three types of maturing ova and concluded that they indicate fractional spawning, yet the most mature ova type was found only in a few ripe-appearing females. Evidently final ova maturation occurs nearly simultaneously with spawning so that the probability of catching a completely ripe fish is low.

Maturation

There are no published reports on maturation in vermilion snapper, but Starck and Schroeder's (1971) results on gray snapper agree closely. They wrote that females are mature at age 3 and 190-200 mm SL. Results for vermilion snapper also agree with Starck and Schroeder's findings that *L. griseus* females >375-400 mm SL probably spawn more times each year than smaller ones, and Mosley (1966) observed (from a sample of fish 223-456 mm SL) that early in the spawning season, smaller red snapper, *L. campechanus*, showed less gonad development than larger ones, perhaps indicating earlier spawning by larger fish. Also similar to our results, Quast (1968) showed earlier and longer seasonal gonad maturation with growth in kelp bass.

Earlier spawning by older fish can probably be explained via the interplay between somatic and gonad growth and maintenance. Sexual maturity marks diminished growth in many fishes (Hubbs 1926; Magnuson and Smith 1963; Iles 1974). Female vermilion snapper older than 5 yr (390 mm TL) are beyond the years of most rapid somatic growth (Grimes 1978) and undoubtedly can afford to put more energy into gonad development, even though the energy costs of maintenance are greater for larger fish as well.

Cohen (1976), using a theoretical mathematical model, predicts that if reproductive success depends upon maximizing reproductive biomass, the change in the fraction of reproductive growth (diminished somatic growth and beginning reproductive growth) will occur at a time and mass just prior to maximum growth rate. We used annual length increments and a length-weight relation (Grimes 1978) to derive annual increments in mass, so that we could evaluate how well vermilion snapper fit the optimal timing of reproduction model. The greatest annual growth increment (weight) occurs between age 6 and 7. Age 5, then, is the year of life the model predicts the growth change, and Figure 5 shows that fish age 5 and older reflect the growth change by maturing earlier and being mature for a longer time each reproductive season.

Sex Ratio

The literature on other lutjanids provides little help in interpreting our findings that sex ratios of vermilion snapper vary significantly from 1:1 overall, and throughout life (as measured by length). Camber's (1955) data on red snapper showed a greater proportion of males when small (200-400 mm TL) but a higher percentage of females among larger fish (400 mm TL). Mosley (1966) reported 56% males and 44% females among red snapper (200-400 mm TL). Bradley and Bryan (1974), however, reported a 1:1 ratio for 1,129 adult red snapper (no size range reported), and Starck and Schroeder (1971) gave a 1:1 ratio for 772 gray snapper (including small juveniles to adults).

Wenner (1972) suggested several possibilities to account for unequal sex ratios (i.e., differential mortality, growth, and longevity; sex reversal; sex difference in activity; and in or out migiration from sampling area by one sex). There is no evidence to support any of these explanations in vermilion snapper, except differential mortality and longevity. Our results show conclusively that relative numbers of females begin to increase (to about 60%) at about 250-300 mm TL, further increase to about 70% at 500-550 mm TL, and eventually reach 90% above 550 mm TL (Table 2). These results indicate that males experience greater mortalities above 250-300 mm TL, and Grimes (1978) demonstrated greater longevity for females (no male was older than 8 yr, but females reach at least age 10). It is interesting to note that differential mortality commences approximately coincidentally with the onset of sexual maturity.

Our fecundity estimates agree reasonably well with published results for other lutjanids. Starck

and Schroeder (1971) estimated fecundity for gray snapper and found a 354 mm SL female to contain about 550,000 ova. Using length conversion equations for vermilion snapper (Grimes 1978), the 354 mm SL is approximately equivalent to a 450 mm TL vermilion snapper which would contain about 410,000 ova.

ACKNOWLEDGMENTS

We wish to thank the staff members of the National Marine Fisheries Service (NMFS), Beaufort, N.C., and Jeffery Ross, Virginia Institute of Marine Sciences, for their assistance in collecting fish and taking of data from specimens. C. A. Barans, South Carolina Marine Resources Center, provided juvenile specimens. D. W. Ahrenholz, D. R. Colby, C. S. Manooch, NMFS, and W. E. Fahy, University of North Carolina, Institute of Marine Sciences, contributed much through helpful discussions and advice.

LITERATURE CITED

BAGENAL, T. B., AND E. BRAUM.
1968. Eggs and early life history. *In* W. E. Ricker (editor), Methods for assessment of fish production in fresh waters, p. 166-198. Blackwell Sci. Publ., Oxford.

BEAUMARRIAGE, D. S.
1973. Age, growth, and reproduction of king mackerel, *Scomberomorus cavalla*, in Florida. Fla. Dep. Nat. Resour., Mar. Res. Rep. 1, 45 p.

BÖHLKE, J. E., AND C. C. G. CHAPLIN.
1968. Fishes of the Bahamas and adjacent tropical waters. Livingstone Publ. Co., Wynnewood, Pa., 771 p.

BRADLEY, E., AND C. E. BRYAN.
1975. Life history and fishery of the red snapper (*Lutjanus campechanus*) in the northwestern Gulf of Mexico: 1970-1974. Proc. 27th Annu. Sess. Gulf Caribb. Fish. Inst., p. 77-106.

BREDER, C. M., JR.
1929. Field book of marine fishes of the Atlantic coast from Labrador to Texas. G. P. Putnam's Sons, N.Y., 332 p.

CAMBER, C. I.
1955. A survey of the red snapper fishery of the Gulf of Mexico with special reference to the Campeche Banks. Fla. State Board Conserv., Tech. Ser. 12, 64 p.

COHEN, D.
1976. The optimal timing of reproduction. Am. Nat. 110:801-807.

DE SILVA, S. S.
1973. Aspects of the reproductive biology of the sprat, *Sprattus sprattus* (L.) in inshore waters of the west coast of Scotland. J. Fish Biol. 5:689-705.

ERDMAN, D. S.
1976. Spawning patterns of fishes from the northeastern Caribbean. Dep. Agric., P. R., Cont. Serv. Esp. 3, 36 p.

FAHAY, M. P.
1975. An annotated list of larval and juvenile fishes captured with surface-towed meter net in the South Atlantic Bight during four RV *Dolphin* cruises between May 1967 and February 1968. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-685, 39 p.

FAHY, W. E.
1954. The life history of the northern greenside darter, *Etheostoma belennioides blennioides* Rafinesque. J. Elisha Mitchell Sci. Soc. 70:139-205.

FINKELSTEIN, S. L.
1969. Age at maturity of scup from New York waters. N.Y. Fish Game J. 16:224-237.

GRIMES, C. B.
1978. Age, growth, and length-weight relationship of vermilion snapper, *Rhomboplites aurorubens*, from North Carolina and South Carolina waters. Trans. Am. Fish. Soc. 107:454-456.

HICKLING, C. F., AND E. RUTENBERG.
1936. The ovary as an indicator of the spawning period in fishes. J. Mar. Biol. Assoc. U.K. 21:311-316.

HUBBS, C. L.
1926. The structural consequences of modifications of the developmental rate in fishes, considered in reference to certain problems in evolution. Am. Nat. 60:57-81.

HUNTSMAN, G. R.
1976. Offshore headboat fishing in North Carolina and South Carolina. Mar. Fish. Rev. 38(3):13-23.

ILES, T. D.
1974. The tactics and strategy of growth in fishes. *In* F. R. Harden Jones (editor), Sea fisheries research, p. 331-345. Wiley, N.Y.

LAROCHE, W. A.
1977. Description of larval and early juvenile vermilion snapper, *Rhomboplites aurorubens*. Fish. Bull., U.S. 75:547-554.

LEGGETT, W. C., AND J. E. CARSCADDEN.
1978. Latitudinal variation in reproductive characteristics of American shad (*Alosa sapidissima*): evidence for population specific life history strategies in fish. J. Fish. Res. Board Can. 35:1469-1478.

LONGLEY, W. H., AND S. F. HILDEBRAND.
1941. Systematic catalogue of the fishes of Tortugas, Fla., with observations on color, habits, and local distribution. Pap. Tortugas Lab. Carnegie Inst. Wash. 34, 331 p.

MACER, C. T.
1974. The reproductive biology of the horse mackerel, *Trachurus trachurus* (L.) in the North Sea and English Channell. J. Fish Biol. 6:415-438.

MACINTYRE, J. G., AND J. D. MILLIMAN.
1970. Physiographic features on the outer shelf and upper slope, Atlantic continental margin, southeastern United States. Geol. Soc. Am. Bull. 81:2577-2598.

MAGNUSON, J. J., AND L. L. SMITH, JR.
1963. Some phases of the life history of the trout-perch. Ecology 44:83-95.

MOSLEY, F.
1966. Biology of the red snapper, *Lutjanus aya* Bloch, of the northwestern Gulf of Mexico. Publ. Inst. Mar. Sci., Univ. Tex. 11:90-101.

MUNRO, J. L., V. C, GAUT, R. THOMPSON, AND P. H. REESON.
1973. The spawning seasons of Caribbean reef fishes. J. Fish Biol. 5:69-84.

QUAST, J. C.
1968. Observations on the food and biology of the kelp bass, *Paralabrax clathratus* with notes on its sportfishery

at San Diego, California. Calif. Fish Game, Fish Bull. 139:81-108.

RICKER, W. E.
1973. Linear regressions in fishery research. J. Fish. Res. Board Can. 30:409-434.

STARCK, W. A., II, AND R. E. SCHROEDER.
1971. Investigations of the gray snapper, *Lutjanus griseus*. Stud. Trop. Oceanogr. (Miami) 10, 224 p.

STRUHSAKER, P.
1969. Demersal fish resources: composition, distribution, and commercial potential of the continental shelf stocks off southeastern United States. Fish. Ind. Res. 4:261-300.

U.S. DEPARTMENT OF COMMERCE.
1971. Tide tables, high and low water predictions, 1972: east coast of North and South America, including Greenland. U.S. Dep. Commer., NOAA, Natl. Ocean Survey, 290 p.
1972. Tide tables, high and low water predictions, 1973: east coast of North and South America, including Greenland. U.S. Dep. Commer., NOAA, Natl. Ocean Survey, 288 p.
1973. Tide tables, high and low water predictions, 1974: east coast of North and South America, including Greenland. U.S. Dep. Commer., NOAA, Natl. Ocean Survey, 288 p.

WALKER, E. T.
1950. Spawning records of fishes seldom reported from North Carolina waters. Copeia 1950:319.

WENNER, A.
1972. Sex ratio as a function of size in marine crustacea. Am. Nat. 106:321-350.

OBSERVATIONS ON EARLY LIFE STAGES OF ATLANTIC TOMCOD, *MICROGADUS TOMCOD*

R. H. Peterson,[1] P. H. Johansen,[2] and J. L. Metcalfe[1]

ABSTRACT

In southern New Brunswick, tomcod spawn in streams from late December to mid-January. The benthic eggs hatch and newly hatched larvae drift to sea in mid-March to mid-April at which time ocean temperatures are beginning to increase. Larval migration to sea is probably aided by active swimming of larvae to the surface to fill the swim bladder, which must be filled within 24 hours of hatching. Photopositivity of the larvae may assist in guiding larvae to the surface.

Water content and specific gravity of eggs reared in 0‰ were 2.8 mg and 1.030. Eggs reared at 10-30‰ had about 2.3 mg water per egg. Specific gravity of eggs incubated in 10‰ was constant for 27 days (at 2°-4° C) at 1.038, then decreased to 1.033. This decrease is associated with water uptake of 0.5-0.6 mg per egg and elimination of salt. The specific gravity of eggs incubated in 20‰ declined linearly from 1.044 to 1.037, associated with accumulation of 0.2 mg of water and elimination of a greater salt load. The specific gravity of eggs incubated at 30‰ declined linearly from 1.049 to 1.045, associated with 0.1 mg water uptake and apparently insufficient salt elimination. Water uptake and salt excretion problems are minimized for eggs reared in freshwater, and under the experimental conditions described here. Normal development could not occur in continued exposure to 30‰. In natural spawning areas, the incubation medium is freshwater for most of the total cycle, with seawater invading the area only at extreme high tide. The salinity tolerance of tomcod eggs is compared with that of freshwater and marine fish eggs in general.

Calculation of specific gravity of egg solids may prove a useful indirect way to investigate salt regulation in fish eggs.

The Atlantic tomcod, *Microgadus tomcod* (Walbaum), is an anadromous species of coastal streams from Newfoundland to Virginia. Adults ascend the lower reaches of southern New Brunswick streams in December and January. These spawning migrations form the basis for a recreational ice fishery in some larger rivers. An annual commercial catch of about 200 t is said to be taken from inshore waters of the northwest Atlantic (Scott and Crossman 1973). Local dip net fishermen take numbers of spawners for both human and animal consumption.

Details of the life history of the early stages (e.g., time of hatching, time of descent into saltwater) have been little studied. Leim (1924) observed that eggs would hatch in freshwater or saline water, but larvae would survive only in saline water. Booth (1967) found sperm motility to be maximal in low salinities, and that salinities of 0-15‰ permitted the highest percentages of eggs to develop to the blastula stage. Howe (1971) described the food habits and growth rates of young tomcod in the Weweantic River estuary, Mass.

The early stages of tomcod development have not been studied extensively; therefore, field studies were performed to obtain information on spawning habitat, rates of egg development, and timing of larval descent to saltwater. Tomcod eggs are deposited in areas subject to variable salinities, so the embryonic development and water balance of tomcod eggs reared in several salinities were also investigated to see how the responses of this species compare with those of freshwater and marine species.

METHODS

Field Studies

The mouth and estuary of Frost Fish Creek (frost fish is a local name for tomcod) were chosen as a study area because the stream hosts a large and regular spawning migration of tomcod which is undisturbed except for some local dip net fishing. It is a small stream (2-4 m wide) forming a common estuary with the Digdeguash River in

[1]Fisheries and Environmental Sciences, Fisheries and Oceans Canada, Biological Station, St. Andrews, NB, E0G 2X0, Canada.
[2]Fisheries and Environmental Sciences, Fisheries and Oceans Canada, Biological Station, St. Andrews, New Brunswick; present address: Department of Biology, Queen's University, Kingston, ON K7L 3N6, Canada.

Manuscript accepted September 1979.
FISHERY BULLETIN: VOL. 78, NO. 1, 1980.

southwestern New Brunswick, with a midsummer discharge ca. 80 l/s and a drainage area of 570 ha (Symons and Martin 1978; Symons and Harding[3]). The drainage basin is typical spruce-fir boreal forest with no human habitation. Portions of it farther upstream have been recently logged.

Tomcod spawn in a 10 to 15 m stretch at the head of tide in Frost Fish Creek (Figure 1). This area is freshwater for most of the tidal cycle, but has a variable bottom salinity (depending upon the height of the particular tide) during high tide. Extreme neap tides do not invade the spawning area. The stream substrate in the spawning area varies from ledge to boulders and cobbles. Most of the eggs settle in substrate interstices.

[3]Symons, P. E. K., and G. D. Harding. 1974. Biomass changes of stream fishes after forest spraying with the insecticide fenitrothion. Fish. Res. Board Can. Tech. Rep. 432, 47 p. Fisheries and Environmental Sciences, Fisheries and Oceans Canada, Biological Station, St. Andrews, NB E0G 2X0.

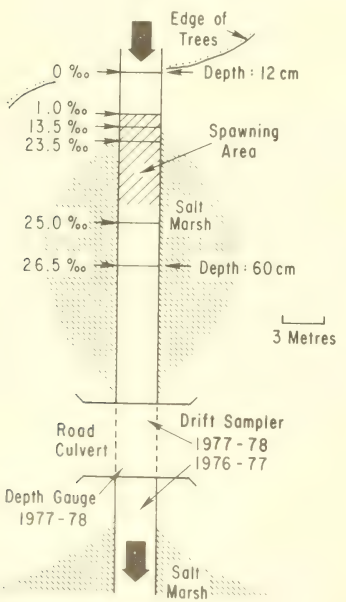


FIGURE 1.—Diagram of tomcod spawning area in Frost Fish Creek in the Digdeguash River estuary, New Brunswick. Depths and salinities are for a "typical" high-tide situation. Salinities were measured at the stream bottom. Hatched area indicates spawning area.

Drift samples were installed downstream of the area of egg deposition (Figure 1) near cessation of spawning (26 Dec. to 2 Jan.) to sample egg and larval drift. The samplers consisted of a galvanized-metal funnel, the narrow opening (5 × 20 cm) facing upstream, with a cloth bag attached to the downstream end (10 × 20 cm). The eggs and larvae accumulated in a 250 ml plastic beaker, with a screened, 2.5 cm diameter hole in one side, clamped to the bag. The sampler was threaded onto an iron rod driven into the stream bottom. A meter stick was installed to measure stream water levels, and stream salinities were measured with a salinity meter. Stream temperatures and drift samples were taken twice weekly at low tide, with the numbers of eggs collected averaged on a per-day basis. Eggs and larvae sampled were preserved in 10% Formalin[4] or 70% ethanol, those preserved in Formalin being cleared later (Galat 1972) to determine degree of development.

One sample of eggs was taken from the area of egg deposition with a Surber sampler in January 1977 to see if development of drifting eggs was the same as those that were not.

Egg Collection

Adults (1 female:2 males) anaesthetized in MS-222 were stripped of eggs and milt in the field. Immediately, the eggs were fertilized by the "dry" method and were washed with stream water 30 s after mixing (temperature at fertilization near 0° C). This water was fresh and was taken from a part of the stream where tomcod were spawning at the time (although spawning may continue into high tide conditions when the water would be of variable salinity). After 1 min the water was changed, and the bottle of eggs was packed in ice and transported to the laboratory. The eggs were transferred to the various incubation salinities 30 min after fertilization. The eggs are weakly adhesive initially, but this adhesiveness disappears if the eggs are separated.

Laboratory Studies

Eggs were incubated in columns of PVC pipe and fittings holding 190 ml of water (Figure 2). Screened floors and lids retained eggs and larvae. Water flowed through the columns at 100 ml/min

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

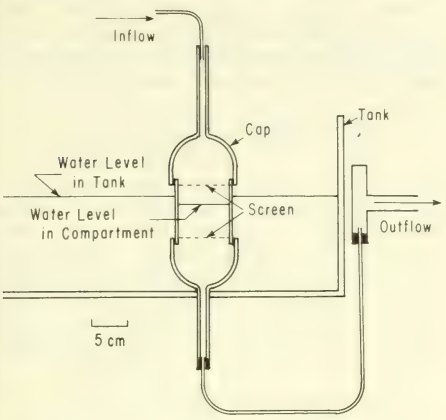


FIGURE 2.—Diagram of incubation chambers used to rear tomcod eggs.

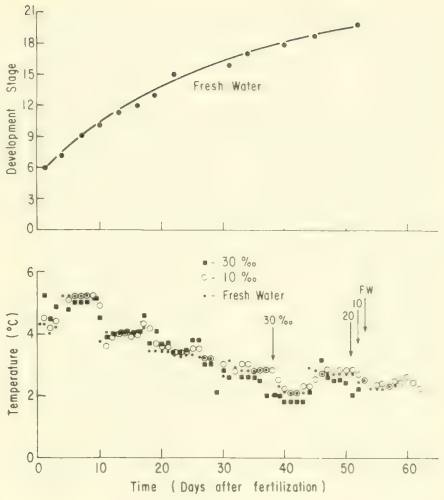


FIGURE 3.—Developmental stages and incubation temperatures for laboratory experiments on tomcod development. Upper panel: Appearance of developmental stages of tomcod eggs incubated in freshwater. Lower panel: Incubation temperatures for tomcod eggs at various incubation salinities. Arrows indicate median hatching dates at each salinity.

(range, 91-111). The columns were immersed in a freshwater bath cooled (2°-4° C) by recirculation of water to refrigerated header tanks. Water flowing to the columns passed through titanium coils in the bath. Water temperature decreased from 4.5° C at the beginning of January to 2.0° C in mid-February (40-d postfertilization), then increased to 2.5° C by the end of February (Figure 3). Eggs were incubated in salinities of 0 (2 columns), 10.1±0.3 (1 column), 20.2±0.6 (1 column), and 30‰ (2 columns). About 250-300 eggs were incubated in each column. Temperature and salinities, by conversion of specific gravity of water with Knudsen's (1962) hydrographical tables, were measured daily.

Columns were checked for egg and larval mortalities every 2-3 d. Every third day, three eggs were removed from each salinity and preserved in 10% Formalin for subsequent study of degree of development. About 100 newly hatched larvae were measured (±0.1 mm) from each salinity and the percentage of deformed larvae noted.

Water content of 10 eggs (combined) from each salinity was measured every fifth day by measuring loss of weight after drying for 16 h at 40° C under vacuum. Specific gravities (sp. gr.) of eggs were measured by glycerol flotation at 10° C as described by Peterson and Metcalfe (1977). Specific gravity of egg solids was calculated from total sp. gr. and water content where solid sp. gr. = egg dry wt/(egg vol. − vol. H_2O), egg vol. = wet wt/sp. gr., and vol. H_2O = water content/sp. gr. of H_2O. Egg diameters were measured microscopically to the nearest 10 μm. Buoyancies of newly hatched larvae, due to air content of the swim bladder, were measured by a Cartesian diver technique (Saunders 1965).

Photic responses of larvae were observed by placing groups of five larvae in a Petri dish, half of which was painted black, on a finger bowl full of ice. Uniform overhead illumination was used.

Statistical Procedures

Differences in water content and dry weights among eggs incubated in the various salinities were tested by one way ANOVA with individual differences detected by means of Duncan's Multiple Range Test. Changes in water content and dry weights during larval development were analyzed by linear regression methods.

RESULTS AND DISCUSSION

Developmental Stages

To assess development of eggs under natural conditions, a series of embryological stages was constructed (Table 1; Figure 3, lower) based on systematically sampled, laboratory-reared eggs. We attempted to make them consistent with those published previously for other species (e.g., Bonnet 1939 for Atlantic cod), although comparisons were difficult in more advanced embryos. For example, Atlantic cod lack a well-differentiated lower jaw at hatching, but it is well developed in tomcod. The stages are also referred to comparable figures in Hardy (1978:278-289) where possible (Table 1). Sampling eggs more frequently would have been useful in some instances; e.g., many anatomical features appeared between days 10 and 13, and are grouped into stage 11. The earliest stages were missed by taking the first sample at 24 h. Stages 3-6 were observed from field samples.

TABLE 1.—Summary of development stages and day of first appearance of anatomical features for tomcod eggs incubated at different salinities. For temperature regime see Figure 3. The stages are for eggs developing in freshwater. Stages 3-5 and 9 were observed in field-collected material only.

Stage	Description	Day of first appearance at: 0‰	10‰	20‰	30‰	Corresponding stage designation by Hardy (1978)
1	Prior to first cleavage	<1	<1	<1	<1	—
2	2 cells	<1	<1	<1	<1	168B
3	4 cells	<1	<1	<1	<1	—
4	8 cells	<1	<1	<1	<1	168C
5	16 cells	<1	<1	<1	<1	—
6	Large celled morula	<1	<1	<1	<1	168E
7	Small celled morula	4	4	4	4	168H
8	Embryonic axis	7	7	7	7	168J
9	Küpfer's vesicle and first somite	—	—	—	—	168E
10	Notochord	10	10	10	10	—
	Optic vesicle	10	10	10	10	169G
11	Eye lens	13	13	13	16	169K
	Ear placode	13	13	13	16	—
	Pericardium	13	13	13	19	—
	Brain lobes differentiating	13	13	13	22	—
	Fin fold	13	13	13	16	—
12	Pectoral fin buds, axial pigmentation	16	16	16	28	170E
13	Eye faintly pigmented	19	19	19	19	170G
14	Gill slit	22	22	22	22	—
	Swim bladder	22	22	25	28	—
15	Nasal placodes	25	25	31	none	—
16	Beginning of pronounced snout	31	31	31	none	171A
17	Lower jaw, mouth not opened	34	34	34	34	171B
18	Mouth can be or is open	37	37	37	—	171C
19	Pigment on lower jaw	45	46	—	—	172A
20	Hatching	—	—	—	—	172A

Irregularities in development were seen in the later stages of development at 30‰. The snout failed to develop normally, and the development of pectoral fin buds and brain lobes was delayed.

Field Observations

Largest numbers of tomcod eggs were sampled by the drift samplers (Figures 4, 5) in the 15- to 20-d period after spawning. The numbers correlated fairly well with stream water level for 1977-78 when water levels were measured (Figure 5). Largest numbers of drifting eggs may also be related to spawning activity rather than stream water levels per se. Typical numbers of eggs col-

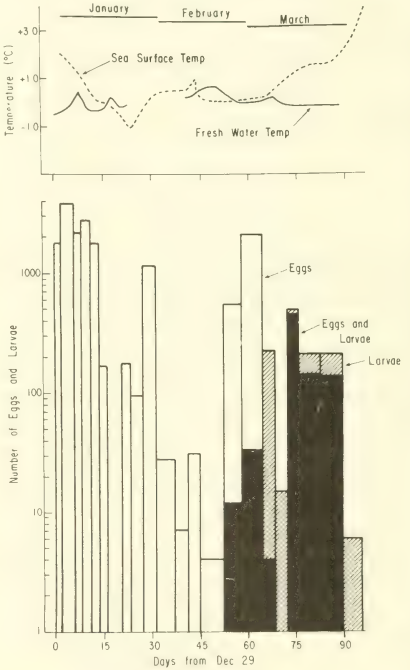


FIGURE 4.—Movements of tomcod eggs and larvae out of Frost Fish Creek. Upper: Environmental conditions and numbers of sampled tomcod eggs and larvae are shown for the 3 mo of egg and larval stream residence in 1976-77. Freshwater temperatures (solid line) and sea surface temperatures (dashed line) for January-April 1976-77. Lower: Histogram of numbers of tomcod eggs and larvae caught in drift samplers. Open bars, eggs; solid bars, eggs and larvae; hatched bars, larvae.

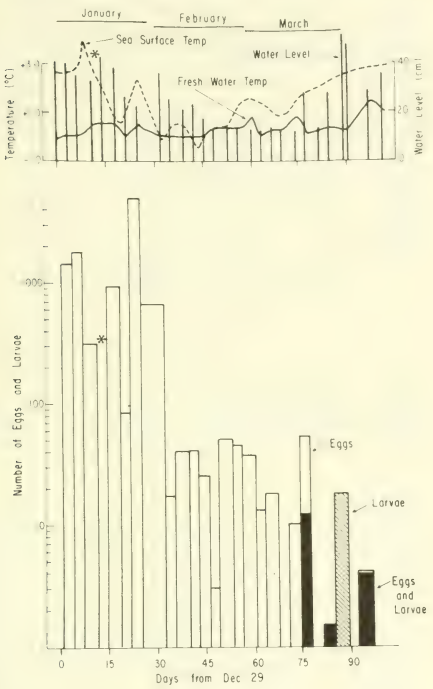


FIGURE 5.—Similar to Figure 4 but for 1977-78. Upper panel includes water levels (vertical bars). Asterisk indicates occurrence of a winter freshet, at which time drift samplers were washed out.

lected ranged from a few hundred to a few thousand per 24 h during these first 15-20 d. In mid-February, stream flow rates decreased as the precipitation accumulated in snow and ice. Typical numbers of eggs sampled/24 h during this period were 10-100. Hatching occurred in March and April (Figures 4, 5). Larvae began to be captured somewhat earlier in 1976-77 and were taken in greater numbers than in 1977-78. This latter phenomenon is thought to be because the sampler was totally submerged in 1977-78, whereas part of it was emergent in 1976-77. Larvae probably emigrate into saltwater near the surface immediately after hatching, as will be discussed in a later section and may have passed over the submerged sampler in 1977-78. Some of the earliest larvae may have hatched in the samplers as a result of warming on the return to the laboratory. These larvae appeared normal and viable. The hatching period in nature corresponded to rising stream water levels in late March in 1977-78. Sea surface temperatures had also risen to 3.0°-4.0° C during fry emigration. Catches of larvae terminated in early to mid-April of both years.

The earliest stages of development obtained in the drift samplers were stage 3 and 4 eggs (Figure 6), owing to lag from spawning to sampling. By the third week of January the embryonic axis was discernible in most eggs sampled. By mid-February, eyes and body axis had become pigmented, nasal placodes and fin fold were appearing, and the tail had curled past the posterior

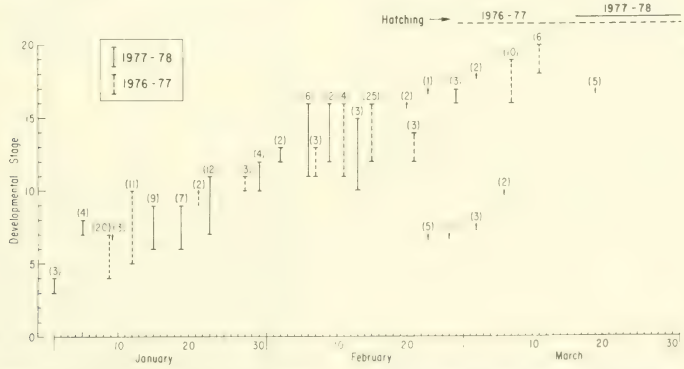


FIGURE 6.—Stages of embryonic development for eggs sampled from Frost Fish Creek with drift samples in 1976-77 and 1977-78. Vertical bars indicate ranges of development observed. Numbers of eggs inspected are in parentheses. Small arrows indicate samples where all eggs were at the same stage.

margin of the eye. Hatching began in late February to mid-March. A series of relatively early stage eggs was also obtained in late February to mid-March 1978 (Figure 6), indicating a possible second spawning of tomcod in late January to early February.

Laboratory Observations

Survival to Hatch and Length at Hatching

Tomcod egg survival to hatching was highest in freshwater (Table 2). Fifty-eight percent of the freshwater eggs hatched, compared with 50, 37, and 13% at 10, 20, and 30‰ salinities, respectively. About half of the mortality at 0 and 10‰ occurred at about day 30 (stage 15). Above 10‰ high mortality also occurred at earlier stages of development.

TABLE 2.—Percentage survival to hatching, total larval length at hatching, and median time to hatch for tomcod eggs incubated at four salinities. Standard deviations are given for larval lengths.

Item	0‰	10‰	20‰	30‰
Percentage egg survival to stage 19	70	73	48	21
Percentage hatched	58	50	37	13
Mean length at hatching (mm)	7.56±0.69	7.25±0.31	6.31±0.44	—
Number of larvae measured	165	104	85	
Time to median hatch (d)	54	51	51	38

Larvae hatched in freshwater were significantly longer than those from higher salinities (7.54 mm for freshwater vs. 7.25 and 6.31 mm at 10 and 20‰, respectively). Larvae at 30‰ had severe spinal curvature and could not be measured accurately. Hatching was earlier at the higher salinities.

The developmental success of tomcod eggs varied with salinity, so various parameters associated with water balance were measured on eggs reared at 0, 10, 20, and 30‰. These parameters are all interdependent so that changes in one may result in concomitant changes in others.

Specific Gravity

The sp. gr. of freshwater (FW) eggs was constant throughout development (Figure 7) at 1.030, implying that weight and volume were not changing or that they were changing in such a way that the sp. gr. was constant. In contrast, eggs incubated at 20 and 30‰ decreased in sp. gr. throughout development. Specific gravity at 10‰ was constant for the first 25 d of incubation, then decreased linearly. The sp. gr. of water at 10, 20, and 30‰ (10° C) are 1.009, 1.017, and 1.024, so that eggs were denser than the incubation medium at all salinities and by approximately the same amount. For example, the sp. gr. of FW eggs is 1.030 compared with 1.000 for freshwater, a difference of 0.03 sp. gr. units. The sp. gr. of 20‰ eggs (extrapolated to 0 time at 20‰ from Figure 7) is 1.045 compared with 1.017 for the incubation medium, again a difference of 0.03 sp. gr. units. Changes in sp. gr. may be associated with changes in water content, loss of solids through metabolism, change of salt content of eggs, or a combination of these factors.

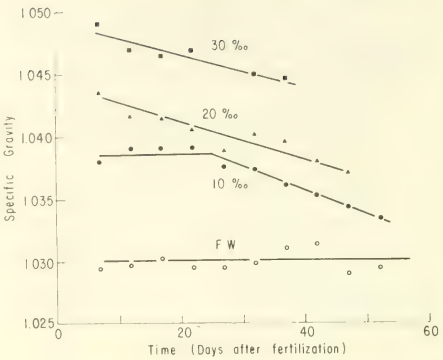


FIGURE 7.—Specific gravity of tomcod eggs incubated at various times from fertilization at various incubation salinities. Each point is based on the mean of measurements made on 10 eggs. Lines fitted by eye. FW = freshwater.

Water Content

Mean water content of FW eggs was 2.83 mg/egg (Table 3) with no trends throughout development. The water content and percentage water content of FW eggs for the first 27 d of development were significantly higher than the values obtained at the other incubation salinities ($P<0.05$, ANOVA, Duncan's Multiple Range Test). The percentage water content increased from 86.4 to 89‰ over the final 25 d of egg development, attributable to decreases in egg dry weight (Tables 4, 5).

There were no significant differences among the percentages of water content of eggs reared at the three higher incubation salinities for the first 27 d

TABLE 3.—Water content (milligrams per egg) and percentage water (parentheses) in tomcod eggs at various incubation salinities and days from fertilization. Each value represents 10 eggs. Sampling periods were fewer at 20 and 30‰ due to earlier hatch.

Days of incubation	0‰	10‰	20‰	30‰
9	2.86(86.7)	2.19(82.3)	2.50(84.7)	2.35(81.9)
12	2.87(87.2)	2.14(84.3)	2.48(83.5)	2.32(82.9)
17	2.72(86.6)	2.36(81.9)	2.47(83.4)	2.54(83.6)
22	2.94(85.5)	2.22(81.5)	2.39(83.9)	2.29(79.8)
27	2.78(86.1)	2.34(83.9)	2.30(82.7)	2.40(82.2)
27-d mean	2.83(86.4)	2.25(82.8)	2.43(83.6)	2.38(82.0)
32	2.78(86.8)	2.40(84.5)	2.41(84.0)	2.42(83.0)
37	2.87(87.5)	2.44(85.3)	2.44(84.5)	2.55(84.7)
42	2.86(89.4)	2.66(86.0)	2.60(86.1)	—
47	2.88(87.8)	2.58(85.4)	2.65(85.8)	—
52	2.76(89.0)	2.91(88.2)	—	—
Newly hatched larvae	1.41(85.5)	—	—	—

The water content of newly hatched FW larvae was 1.41 mg (85.5%), so about half of the water in the FW egg is associated with perivitelline fluid and zona radiata.

Dry Weight

No measurable change in egg dry weight occurred over the first 27 d of incubation (Table 4). A one way ANOVA indicated significant differences among the mean dry weights for the first 27 d of incubation ($F = 3.9$, $P<0.05$). The mean dry weight of 30‰ was significantly greater than those of FW and 20‰ eggs (Duncan's Multiple Range Test).

TABLE 4.—Dry weights (mg) for various incubation salinities and times from fertilization (d). Each value is averaged from 10 pooled eggs. Values to the left of the bracket for the first 27 d of development are means for that period.

Days of incubation	Incubation salinity (‰)			
	0	10	20	30
9	0.44	0.47	0.45	0.52
12	0.42	0.40	0.49	0.48
17	$\pm^{0.45}_{0.03}$ 0.42	$\pm^{0.47}_{0.05}$ 0.52	$\pm^{0.47}_{0.02}$ 0.49	$\pm^{0.52}_{0.04}$ 0.50
22	0.50	0.50	0.46	0.58
27	0.45	0.45	0.48	0.52
32	0.42	0.44	0.46	0.51
37	0.41	0.42	0.46	0.46
42	0.34	0.40	0.42	—
47	0.36	0.44	0.44	—
52	0.34	0.39	—	—
Newly hatched larvae	0.25	—	—	—

TABLE 5.—Statistical parameters for regressions of percentage water content vs. time (d) and dry wt vs. time (data given in Tables 3, 4). Times are for days 27-52, inclusive. b = slope of regression equation, r = correlation coefficient, df = degrees of freedom.

Regression	Parameter	Incubation salinity (‰)		
		0	10	20
% H_2O vs. time	b(%/d)	0.10	0.17	0.13
	r	0.80	0.91	0.93
	df	4	4	3
	t	2.72	4.53	4.47
	P	~0.05	<0.025	<0.05
Dry wt vs. time	b(mg/d)	−0.0046	−0.0018	−0.0024
	r	0.96	0.70	0.83
	df	4	4	3
	t	3.55	3.92	2.60
	P	<0.025	<0.025	<0.1

Dry weight decreased significantly over the last 25 d (Tables 4, 5). This decrease was greatest in freshwater, about 0.1 mg/egg compared with 0.07 and 0.04 at 10 and 20‰, respectively. Although sample size is inadequate for statistical analysis, it would appear that the 30‰ eggs lost about 0.05 mg/egg. Yolk content of newly hatched larvae was not measured; however, larvae hatched from higher incubation salinities appear to have more yolk (Figure 8), an observation supported by the fact that hatching is earlier at higher salinities. The lesser amount of yolk of FW eggs is in agreement with the greater loss of solids by these eggs.

About 25% of the dry weight of FW eggs is lost at hatching, and is thus contributed by the chorion and the perivitelline fluid.

of incubation. The water content of 10‰ eggs increased over the last 25 d of incubation at 0.023 mg/egg per d ($P<0.05$, Tables 3, 5), until the water content at hatching approached that of FW eggs. The 20‰ eggs took up water after 27 d incubation at 0.018 mg/egg per d ($P<0.01$), but the water content of these eggs was still lower than for eggs incubated in FW and 10‰. The 30‰ eggs may have taken up slight amounts of water, but the data are insufficient to be tested statistically.

Egg Diameter

The diameters of 10 eggs from each incubation salinity were measured at the time intervals indicated in Table 6. There was no indication of any change in egg diameter with length of incubation (Table 6), so that the water uptake at the three

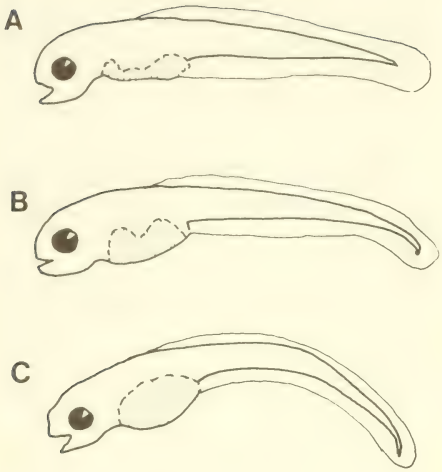


FIGURE 8.—Newly hatched tomcod larvae from various incubation salinities. Note the larger amounts of yolk remaining, the higher the salinity of incubation. A. Freshwater; B. 10‰; C. 20‰. Yolks have shrunk due to (Formalin) fixation effects. Magnifications 13×.

TABLE 6.—Egg diameters (millimeters) for various incubation salinities and incubation times. Each value is the mean of 10 measurements. v = calculated egg volume (microliters). Standard deviations given in parentheses.

Days of incubation	0‰	10‰	20‰	30‰
4	1.85(0.06)	1.79(0.08)	1.77(0.05)	1.81(0.09)
12	1.86(0.04)	1.76(0.07)	1.75(0.06)	1.76(0.04)
17	1.87(0.05)	1.75(0.05)	1.79(0.05)	1.80(0.04)
22	1.89(0.04)	1.77(0.05)	1.76(0.05)	1.78(0.05)
27	1.84(0.07)	1.75(0.05)	1.76(0.05)	1.76(0.04)
32	1.89(0.02)	1.74(0.05)	1.78(0.06)	1.78(0.05)
37	1.90(0.05)	1.77(0.05)	1.78(0.05)	1.78(0.06)
42	1.93(0.05)	1.82(0.04)	1.81(0.05)	—
47	1.84(0.04)	1.81(0.04)	1.76(0.06)	—
52	1.86(0.07)	1.79(0.05)	—	—
$\bar{x}$	1.87	1.78	1.77	1.78
v	3.47	2.86	2.84	2.83

higher salinities toward the end of the incubation period did not lead to measurable swelling, although slight swelling within experimental error probably occurred. The mean diameters of FW, 10, 20, and 30‰ eggs were 1.87, 1.78, 1.77, and 1.78 mm, respectively. The standard deviations for lots of 10 eggs varied from 0.02 to 0.09 mm, and were 0.04-0.05 in most cases. The greater diameter of the FW eggs is no doubt related to the higher water content of these eggs.

Specific Gravity of Egg Solids

The sp. gr. of FW egg solids (lipids included) was constant at 1.27 for the first 27 d of incubation (Figure 9), then rose linearly to about 1.36 just before hatching. This increase in sp. gr. of egg solids may be due to increase in compact tissue, such as cartilage. It could also reflect a rapid increase in embryonic tissue and a corresponding decrease in yolk solids. The sp. gr. of solids of Atlantic salmon alevins also increases during development (Peterson and Metcalfe 1977). This was shown to be due to increase in embryonic mass, the solids of which had a higher sp. gr. than did yolk solids.

The sp. gr. of 10‰ egg solids was identical to that of FW eggs throughout. Apparently, insufficient salt penetrated these eggs to change the solids' sp. gr. measurably. This apparent lack of difference between FW and 10‰ eggs should be accepted with some caution, since an error of 0.01 mg/egg in estimating dry weight (averaged over the first five measurements) could result in a shift in solids' sp. gr. by 0.2 units. Since the dry weight of 10‰ eggs was some 0.02 mg greater than that of FW eggs (Table 4), some salt may well have entered the 10‰ eggs.

The sp. gr.'s of egg solids for 20 and 30‰ eggs during early development were much higher than for the two lower salinities (Figure 9), and they

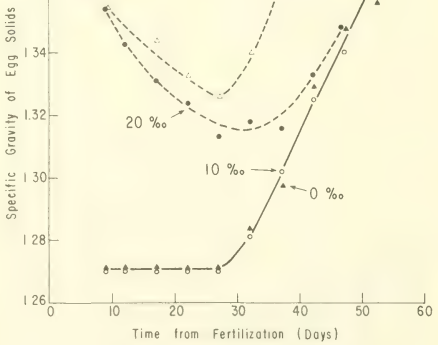


FIGURE 9.—The specific gravity of egg solids (as calculated from water content and egg specific gravity) at various times from fertilization for various incubation salinities. Lines fitted by eye.

decrease with time until a minimum is attained at 27 d postfertilization. The sp. gr. then rose again, as for eggs reared at 0 and 10‰. The decrease in egg solids' sp. gr. from fertilization to day 27 at 20 and 30‰ may be due to more efficient salt elimination as the embryo grows. After 27 d the decrease due to salt elimination is more than balanced by increases due to factors postulated above for FW eggs. Apparently, eggs reared at 20‰ were successful in eliminating salt, because the sp. gr. of their egg solids tends to converge with that for eggs reared at lower salinities. At 30‰, however, the embryos appeared to be unable to eliminate excess salt successfully because the solids' sp. gr. never approached those for eggs reared at lower incubation salinities. The 30‰ eggs hatch earlier than those incubated at lower salinities, perhaps in response to high salt concentrations. As mentioned previously, they were abnormally developed.

The higher sp. gr. of egg solids at 30‰ would require that 15% of the solids be excess salt (using the formula $1.27a + 1.8(1-a) = 1.35$; where a = proportion of egg solids that is not salt; 1.8 = sp. gr. of salt, 1.27 = sp. gr. of FW egg solids, 1.35 = sp. gr. of 30‰ egg solids). This amounts to about 0.08 mg. This is reasonably close to the increase in dry weight of 30‰ eggs over FW eggs (0.07 mg). The decrease in sp. gr. of 30‰ egg solids to its minimum of 1.33 would require the loss of 0.02 mg of salt.

Newly hatched larvae in freshwater that did not have access to the water surface had an sp. gr. of 1.032, which is nearly identical to that of eggs incubated in freshwater. If larvae were permitted access to air at the water surface, the sp. gr. declined within 7 h to 1.01, coincident with ingestion of air into the swim bladder. Newly hatched larvae were observed swallowing air at the surface. The filling of the swim bladder was investigated further with a Cartesian diver technique. Larvae that had access to air floated at a flotation pressure (Saunders 1965) of 154 mm Hg (130-170, $n = 6$) (0.8 atm). Those that had been denied access to air for 24 h failed to float at 675 mm Hg (645-685, $n = 15$), corresponding to 0.1 atm (the greatest vacuum attainable with the apparatus). No air was observed in the swim bladder of these larvae. These larvae were then allowed access to the surface overnight. When tested subsequently, none floated at 675 mm Hg, nor was air observed in the swim bladder. These latter larvae, unlike larvae with air in the swim bladder (that spend most of their time near the surface), stayed on the bottom of the container.

Newly hatched larvae were photopositive as tested in a half-blackened Petri dish. In two trials, 78% (39/50) and 64% (16/25) larvae were observed in the lighted (unpainted) half of the Petri dish. When the dish was kept in darkness, 46% (23/50) and 36% (9/25) larvae were observed in the unpainted half. Larvae were commonly observed to aggregate near the lighted sides of rearing containers.

GENERAL DISCUSSION

The changes that occurred in eggs reared in various salinities will first be summarized:

Eggs reared in freshwater consisted of 2.8 mg water, sufficient for the embryo's needs, being constant throughout development. The egg sp. gr. was also constant despite decrease in solid materials (ca. 0.1 mg)—the egg diameter should therefore decrease slightly (about a 1.7% decrease is required), although this was not observed, as it is within experimental error.

Eggs reared in 10‰ salinity have about 2.2 mg water for the first month of development, but take up an additional 0.5-0.6 mg in the later stages of development, due to the greater water requirements of embryonic tissue. Some of this uptake may also be associated with formation of fluid filled body cavities (Zotin 1965). This water uptake was associated with a decreased egg sp. gr. The 10‰ eggs may have a slight salt load which is probably eliminated in the later developmental stages. The egg dry weight declined by only 0.07 mg, and newly hatched 10‰ larvae may have larger yolks than do those in 0‰ (Figure 9).

Eggs reared in 20‰ salinity had a water content equal to or greater than that of 10‰ eggs in the early stages of development, but had to tolerate a higher salt load (ca. 0.04 mg/egg) as a result. Egg sp. gr. declined throughout development due to salt elimination as the embryo developed and to accumulation of about 0.2 mg water during the later developmental stages. Advanced embryos eliminated much of the initial salt load as the egg solid sp. gr. of late stage eggs is nearly identical to that of eggs reared at lower salinities. The concept of salt elimination seems reasonable, but is subject to some uncertainty in these experiments because the solids associated with the chorion and perivitelline fluid are included in the estimates of

solids sp. gr. These compartments of the egg obviously would have no capacity for elimination of salts. Egg dry weight declined by only 0.04 mg at hatching as newly hatched 20‰ larvae appear to have even more yolk than 10‰ larvae (Figure 8). The 20‰ curve in Figure 9 suggests that salt elimination began very early and increased as the embryo grew. It is probable that at least the early salt elimination had a cellular rather than organ basis.

Eggs reared in 30‰ salinity also had a water content similar to those reared at 10 and 20‰, but the salt load was high. Water accumulation during the later developmental stages was low (ca. 0.1 mg). The sp. gr. of egg solids goes down over the first 27 d of development, indicating some elimination of salt. The pattern during the later stages of development is strikingly different from that at 20‰ in that the solids' sp. gr. again rose to about 1.37 at 37 d of incubation at which point the larva hatched. Problems with salt balance and osmoregulation may have led to the deformities and early hatching. The dry weight of 30‰ eggs decreased only slightly during development.

It has been shown, for the eggs and larvae of some marine organisms, that the salinity in which fertilization and the earliest stage of development occur may influence development and growth of subsequent stages in the life history (Kinne 1962). It is therefore possible that eggs fertilized in water of higher salinity might have responded differently to the various experimental salinities. Booth (1967) obtained data suggesting that fertilization could occur in salinities as high as 15‰. It is notable, however, that the eggs of *Cyprinodon macularius* in Kinne's experiments were allowed to develop 3-6 h in the spawning salinity, and at a higher temperature (27° C) than was the case for the tomcod experiments. It is probable that the eggs of *C. macularius* had developed further before experimentation.

The tomcod's early life history seems adapted to the hydrodynamics of streams in which it spawns. Spawning migrations occur in late December to early January while water levels are still high from the fall freshets. The eggs develop throughout midwinter when water levels are low, thus minimizing loss of eggs from the stream, then hatch when water levels are rising coincident with the early snow melt. The higher water levels during hatching would ensure rapid flushing of larvae into the estuary. Newly hatched larvae probably rise to the stream surface soon after hatching and ingest air into the swim bladder, with possibly the positive response to light facilitating surfacing. This behavior of newly hatched larvae would also ensure rapid flushing into the estuary.

The continuous drift of eggs out of the stream is somewhat puzzling. Most eggs taken in the drift samples were alive and apparently developing normally. These perhaps are eggs which had been deposited where they were likely to be taken up into suspension. In support of this suggestion, egg drift was positively correlated with stream level. Whether these eggs continue to develop would depend in part upon the salinity conditions where they finally settle and the ambient salinity during earlier development. Laboratory results indicate that less than full salinities are required for normal development from fertilization, but the effects of variable salinities on tomcod egg development were not investigated.

The tomcod egg resembled those of freshwater species (rather than marine species) in regard to salt tolerance, assuming that the responses reported here are typical. Eggs of brook trout exhibit increased mortality above 6‰ salinity with total mortality at 12‰ (Sutterlin et al.[5]). Species such as *Abramis* will hatch in salinities up to 20‰, although 2.5-5‰ is optimal (Holliday 1969). With the tomcod, between 20 and 30‰ salinity appears to be the upper limit for production of normal larvae. By way of contrast, eggs of several marine species have been hatched in salinities up to 60‰ (cod, herring, plaice), although optima are usually in the 25-30‰ range (Holliday and Blaxter 1960; Holliday 1965).

Eggs of marine species tend to swell at low salinities (usually <15‰); above this salinity egg diameter is constant (Holliday 1965; Solemdal 1967). Tomcod eggs require salinities of <10‰ for noticeable swelling to occur.

Several parameters measured (water content, dry weight, solids' sp. gr., and egg sp. gr. for 10‰ incubation) begin to change dramatically at about 27 d of incubation. In relation to embryonic development it seems probable the embryonic mass is beginning to increase dramatically at this point, resulting in the noted physiological changes. Perhaps these changes are linked to the high mortality occurring at this stage of development.

[5]Sutterlin, A. M., P. Harmon, and H. Barchard. 1976. The culture of brook trout in salt water. Fish. Mar. Serv. Res. Dev. Tech. Rep. 636, 21 p. Fisheries and Environmental Sciences, Fisheries and Oceans Canada, Biological Station, St. Andrews, NB E0G 2X0.

Zotin (1965) reported that eggs of freshwater teleosts (e.g., loach, zander (*Lucioperca*)) took up no water after water hardening until the chorion began to stretch due to weakening by the hatching enzyme. The mullet egg took up water during the second half of development during which time the perivitelline space first appeared. With the tomcod, water uptake occurred in the latter stages of development in the three higher salinities. It is not known where this water was distributed within the egg, but it was probably incorporated into embryonic tissue.

It is inferred, from calculated specific gravity of egg solids, that tomcod embryos osmoregulated to some degree, becoming more proficient as development proceeded. This may be simply a function of embryonic size, resulting in more osmoregulating tissue. It has been suggested by Holliday (1965) that plaice embryos can regulate osmotic concentration after gastrulation, which occurs in 9 d or less in these tomcod eggs. Holliday (1969) also showed that flounder eggs could regulate yolk sodium from fertilization. Unfortunately, we did not make measurements here before 9 d of incubation.

Holliday and Blaxter (1960) and Forrester and Alderdice (1966) observed development to proceed faster at higher salinities for herring and Pacific cod, respectively. While tomcod hatched earlier at higher salinities, there is little suggestion that development occurred more rapidly. Rather, it appeared that the freshwater larvae grew larger prior to hatching. Some structures were delayed, or never appeared in 30‰ embryos, but this is due to abnormal development at this salinity. Abnormal development has frequently been recorded at abnormally high salinities. Usually the deformities are skeletal as are observed for tomcod, or involved body cavity deformities (Holliday 1965; Alderdice and Forrester 1971).

Although the tomcod is a physoclist species, the pneumatic duct is apparently functional in the newly hatched larva. In <24 h the duct is closed, and the larva can no longer fill the swim bladder by air ingestion. Larval loss of the pneumatic duct has been implied for physoclists generally (Harden Jones 1957). Whether or not the duct is utilized in initial filling of the bladder is apparently quite variable (Johnston 1953; Schwarz 1971).

ACKNOWLEDGMENTS

We wish to acknowledge P. Harmon for assisting in some aspects of field studies; P. W. G. McMullon and F. Cunningham for performing the photography and drafting; A. Sreedharan for providing statistical analyses of the data; and D. W. McLeese and M. J. Dadswell for reviewing the manuscript.

LITERATURE CITED

ALDERDICE, D. F., AND C. R. FORRESTER.
1971. Effects of salinity, temperature, and dissolved oxygen on early development of the Pacific cod (*Gadus macrocephalus*). J. Fish. Res. Board Can. 28:883-902.

BONNET, D. D.
1939. Mortality of the cod egg in relation to temperature. Biol. Bull. (Woods Hole) 76:428-441.

BOOTH, R. A.
1967. A description of the larval stages of the tomcod, *Microgadus tomcod*, with comments on its spawning ecology. Ph.D. Thesis, Univ. Connecticut, Storrs, 53 p.

FORRESTER, C. R., AND D. F. ALDERDICE.
1966. Effects of salinity and temperature on embryonic development of the Pacific cod (*Gadus macrocephalus*). J. Fish. Res. Board Can. 23:319-340.

GALAT, D. L.
1972. Preparing teleost embryos for study. Prog. Fish-Cult. 34:43-48.

HARDEN JONES, F. R.
1957. The swimbladder. *In* M. E. Brown (editor), The physiology of fishes, Vol. II, p. 305-322. Acad. Press, N.Y.

HARDY, J. D., JR.
1978. Development of fishes of the mid-Atlantic Bight, an atlas of egg, larval, and juvenile stages. Vol. II, Anguillidae through Syngnathidae. U.S. Fish Wildl. Serv., Biol. Serv. Program Chesapeake Biol. Lab. FWS-OBS-78-12, 458 p.

HOLLIDAY, F. G. T.
1965. Osmoregulation in marine teleost eggs and larvae. Calif. Coop. Oceanic Fish. Invest. Rep. 10:89-95.
1969. The effects of salinity on the eggs and larvae of teleosts. *In* W. S. Hoar and D. J. Randall (editors), Fish physiology, Vol. I, p. 293-311. Acad. Press, N.Y.

HOLLIDAY, F. G. T., AND J. H. S. BLAXTER.
1960. The effects of salinity on the developing eggs and larvae of the herring. J. Mar. Biol. Assoc. U.K. 39:591-603.

HOWE, A. B.
1971. Biological investigations of Atlantic tomcod, *Microgadus tomcod* (Walbaum), in the Weweantic River estuary, Massachusetts, 1967. M.S. Thesis, Univ. Massachusetts, Amherst, 82 p.

JOHNSTON, P. M.
1953. The embryonic development of the swim bladder of the largemouth black bass *Micropterus salmonides salmonides* (Lacépède). J. Morphol. 93:45-47.

KINNE, O.
1962. Irreversible nongenetic adaptation. Comp. Biochem. Physiol. 5:265-282.

KNUDSEN, M.
1962. The determination of chlorinity by the Knudsen method. G. M. Mfg. Co., N.Y., 63 p.

LEIM, A. H.
1924. The life history of the shad (*Alosa sapidissima* (Wilson)) with special reference to the factors limiting its abundance. Contrib. Can. Biol. New Ser. 2:163-284.

PETERSON, R. H., AND J. L. METCALFE.
1977. Changes in specific gravity of Atlantic salmon (*Salmo salar*) alevins. J. Fish. Res. Board Can. 34:2388-2395.

SAUNDERS, R. L.
1965. Adjustment of buoyancy in young Atlantic salmon and brook trout by changes in swimbladder volume. J. Fish. Res. Board Can. 22:335-352.

SCHWARZ, A.
1971. Swimbladder development and function in the haddock, *Melanogrammus aeglefinus* L. Biol. Bull. (Woods Hole) 141:176-188.

SCOTT, W. B., AND E. J. CROSSMAN.
1973. Freshwater fishes of Canada. Fish. Res. Board Can., Bull. 184, 966 p.

SOLEMDAL, P.
1967. The effect of salinity on buoyancy, size and development of flounder eggs. Sarsia 29:431-442.

SYMONS, P. E. K., AND J. D. MARTIN.
1978. Discovery of juvenile Pacific salmon (coho) in a small coastal stream of New Brunswick. Fish. Bull., U.S. 76:487-489.

ZOTIN, A. I.
1965. The uptake and movement of water in embryos. Symp. Soc. Exp. Biol. 19:365-384.

NOTES

OBSERVATIONS OF SEA OTTERS DIGGING FOR CLAMS AT MONTEREY HARBOR, CALIFORNIA

Although the feeding behavior of the sea otter, *Enhydra lutris*, is frequently observed from the surface, few underwater observations of foraging sea otters have been published. Faro (1969) and Houk and Geibel (1974) described the underwater behavior and tool use of sea otters when they removed abalone from rock substrates. Shimek (1977) observed a sea otter foraging for snails and presumably other invertebrates by patting the surface of rocks and feeling into cracks. Shimek also described a sea otter digging up the echiuroid worm, *Urechis caupo*, from a silt and cobble substrate. Further deductions about underwater foraging behavior have been made from collections of abalone shells with the characteristic "otter break" hole in the middle (Wild and Ames[1]) and from observations of aluminum beverage cans bitten by otters to remove octopus (McCleneghan and Ames 1976). Some sea otters can be enticed underwater to take food offered them (pers. obs). However, these latter observations of underwater food manipulation are of limited value because the otters also take items unpalatable to them (e.g., the holothuroid *Stichopus californicus*), and because the otters were clearly interacting with the diver observer. These accounts of underwater foraging indicate that sea otters use primarily tactile sensitivity of the forelimbs to locate and capture prey, whereas all other marine mammals (pinnipeds and cetaceans) use their jaws to capture prey. Radinsky (1968) hypothesized that the sea otter evolved forelimb tactile sensitivity separately from the aonychoid otters.

The large impact of sea otters on Pismo clam, *Tivela stultorum*, populations in California has been documented (Stephenson 1977; Miller et al.[2]), and in Prince William Sound, Alaska, 81% of the food items taken by sea otters were bivalves, especially *Saxidomus gigantea* (Calkins 1978). The Alaskan otters "dug out clams with their forepaws while maintaining a head downward position" in intertidal and shallow subtidal water. However, Shimek's (1977) description is the only detailed underwater observation of sea otters foraging on soft substrate. Detailed observations of sea otters taking prey from soft substrates are more difficult than those on rock, because the otter's disturbance of the bottom often results in clouds of sediment obscuring further vision. In the present account, we describe underwater observations of sea otters digging clams in a silty sand substrate and present information about the impact of this foraging on the distribution and abundance of subtidal clams at Monterey Harbor, Calif.

Observations

In 1976-77 we observed sea otters eating large numbers of the Washington clam, *Saxidomus nuttalli*, primarily in two specific areas of Monterey Harbor (A and B of Figure 1). From vantage points along the floating boat slips and elevated wharves, we observed sea otters at the surface feeding on 211 prey items: *S. nuttalli* (88.6%); the crabs *Pugettia producta* (4.2%) and *Cancer* sp. (3.3%—probably *C. antennarius* or *C. productus*, but not *C. magister*); the rock jingle bivalve *Pododesmus cepio* (1.4%); and unidentified items (2.4%). During spring 1976, as many as four sea otters were foraging at one time in the harbor vicinity, but an average of about one sea otter was observed on 38 counting trips made to the area.

The underwater path of foraging sea otters could often be observed from the surface by following the trail of air bubbles escaping from their compressed fur. The paths of foraging dives made in the inner harbor were often contorted, 50-60 m or more long, and lasted 45-80 s. These dives usually produced no prey, but the prey taken were mostly crabs and rarely clams. On those dives that resulted in the capture of kelp crabs, sea otters usually (eight out of nine dives) finished their search with a swim under 10-20 m of the floating docks in the inner area of the harbor. During scuba dives in this area, we repeatedly observed kelp crabs on the undersides of these floats and rarely elsewhere. It was difficult to observe the paths of

[1]Wild, P. W., and J. A. Ames. 1974. A report on the sea otter, *Enhydra lutris* L., in California. Calif. Dep. Fish and Game Mar. Resour. Tech. Rep. 20, 93 p.

[2]Miller, D. J., J. E. Hardwick, and W. A. Dahlstrom. 1975. Pismo clams and sea otters. Calif. Dep. Fish Game Mar. Resour. Tech. Rep. 31, 49 p.

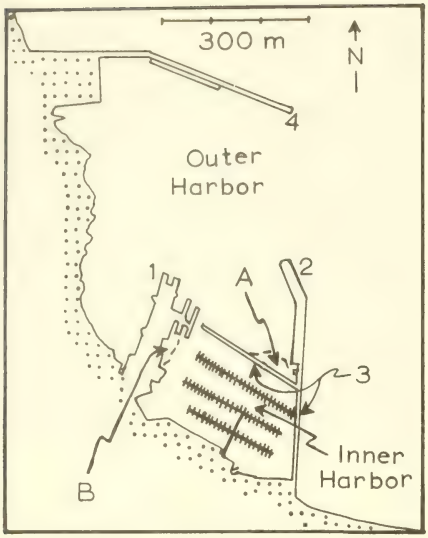


FIGURE 1.—Monterey Harbor, Calif. High densities of clams were foraged by sea otters in areas A and B. 1 = Fisherman's Wharf; 2 = Wharf No. 2; 3 = north and east sea walls of the inner harbor; 4 = breakwater for the outer harbor. (Traced from an aerial photograph in Haderlie and Donat 1978.)

dives made in the middle of the outer harbor, but sea otters usually surfaced without prey 50 m or more from the start of the dive. However, the paths of feeding dives in the two locations where clams were taken in abundance were usually quite short, only 10 m or less.

The usual sequence of dives in the harbor region began with otters making one to three 50-90 s dives that produced no prey. After about 10-20 s on the surface and a little grooming, the otters usually dove again to the same spot. A series of short (25-40 s) dives followed the initial dives, and each of these invariably resulted in a single *S. nuttalli* about 10 cm long. The otters took 30-90 s to open and eat the clams before diving to the same spot. Sometimes they pounded the clams on a rock anvil on their chest; other times they simply twisted or pried the clams open with their teeth. An average of 6 and as many as 19 clams were taken in a single series of these dives. Following such a series, otters usually spent up to 30 min grooming before they swam away, sometimes to forage in a new location.

In spring 1976, we conducted an underwater survey of most of the bottom of the inner and outer harbor, noting variations in the substrate and counting protruding clam siphons in haphazardly tossed ¼ m^2 quadrats. Depths in the harbor ranged from 2 to 8 m, with area A being 4.5 m and area B 2-3 m (Figure 1). The substrate in much of the enclosed inner harbor was black mud and silt, and most of the rest of the harbor (including areas A and B) was silty sand. The two areas where otters fed extensively on clams had high densities of clam siphons: for area A, $\bar{x} = 13.5/m^2$, SD = 8.9, $n = 19$; for area B, $\bar{x} = 9.3/m^2$, SD = 7.2, $n = 16$. The area under Wharf No. 2 adjacent to area A had even higher densities of siphons: $\bar{x} = 17.4/m^2$, SD = 11.9, $n = 18$. However, other areas of the harbor had siphon densities $< 1.0/m^2$, and the black mud of the inner harbor had densities $< 0.04/m^2$. We inserted a slender rod down siphon holes in the substrate until the rod contacted the clam shell, and, with considerable difficulty, we used a stream of freshwater from a garden hose to obtain a few 8-14 cm long clams from area A. We used these specimens to distinguish the two species present by the morphology of the protruding siphons. The species composition in areas A, B, and under Wharf No. 2 were the same: 95% were *S. nuttalli*, 5% were the gaper clam, *Tresus nuttallii*. In this way we also determined that the clams were located 10-50 cm into the substrate and that larger individuals of both species tended to occur at the deeper end of this range in the sediment. We recorded the densities of clam siphons in area A and also in the adjacent area of highest density under Wharf No. 2 at approximately bimonthly intervals from February 1976 to March 1977. The densities and proportions of the two species of clams did not change (ANOVA, $P > 0.05$).

The bottom in the two areas where sea otters took large numbers of clams was littered with hundreds of shells, both on the surface and mixed into the sediments. About 58% of the shells did not have pairs of connected valves, and about one-third of the valves were broken. Of 89 shells sampled, 99% were *S. nuttalli* and 1% were *T. nuttallii*. The bottom topography was hummocky in these areas, and there were many craters 0.5-1.0 m across and 10-15 cm deep. The bottom under Wharf No. 2, where the density of clam siphons was highest, was mixed with debris consisting of chunks of asphalt apparently from resurfacing of the road on the wharf and of clumps of large barnacle, *Balanus nubilus*, tests which had fallen

from the massive barnacles encrusting the pilings. There were considerably fewer craters in this area compared with the adjacent area A, and our attempts to dig into the substrate under the wharf proved difficult as a result of the debris embedded in the sediment.

Sea otters were in the process of foraging on clams during several of the scuba dives in area A. Although these otters were not bothered by our presence under water, attempts to observe precisely how they were capturing clams usually failed because they stirred up large clouds of sediment that obscured all of their activity. When the otters stopped foraging and the clouds of sediment dispersed, a large hole up to 1.0-1.5 m across and 0.5 m deep had obviously resulted from their digging. The sides of these holes were initially nearly vertical, but collapsed within minutes.

Details of a sea otter digging for clams were observed by the first author on a single occasion on 30 March 1977, when a strong current rapidly dispersed the clouds of sediment. Upon observing a young male otter begin a typical sequence of foraging dives in area A, the observer moved along the bottom and approached the digging site from an upstream direction. The otter was clearly visible at a distance of 5 m and was just leaving the bottom after completing the second longer dive of the series. He returned to the bottom within 20 s but abandoned the initial digging site, leaving a small hole about 0.5 m across and 25 cm deep. Instead, on this third dive, he moved immediately to a new spot about 4 m away and began to dig rapidly with his front paws in a fashion very much like a dog, producing a large conical cloud of sediment extending downstream. Digging lasted about 45 s, followed by a 20 s surface interval. On the fourth dive the otter resumed digging in the same spot, and as during all digging periods, he faced into the current. The observer was able to approach < 1 m from the sea otter by creeping up in a prone position on the bottom while the otter substantially enlarged the hole to a short trench about 1 m long, 0.5 m across, and 25 cm deep by digging rapidly with both front paws. His back flippers were moving at a slower rate, which probably helped maintain his position and also appeared to assist in digging. Toward the end of the digging on this dive the otter began to roll repeatedly from side to side to enlarge the front end of the trench laterally, until he apparently encountered a clam and suddenly surfaced for 45 s. On the fifth dive this rapid process of rolling and lateral digging with the front paws continued again for about 30 s until another clam was caught and the activity suddenly stopped. The hole at this time was over 0.5 m deep and the otter's body was entirely below the level of the substrate surface while digging. The otter used this process of lateral digging on three more dives lasting about 30 s each with 40-60 s surface intervals, before the observer ran out of air and surfaced. The trench at that time was over 1.5 m long and remained about 0.5 m wide and deep. The otter terminated the series of feeding dives with one additional dive while the observer was at the surface. It paid no apparent attention to the observer's close presence during the entire series. Simultaneous observations by the second author from the surface indicated that none of the first three dives (including two dives at the first spot) produced a clam, but that each of the six subsequent dives resulted in a single clam. The otter did not use a rock to open the clams.

Discussion

In 1966, prior to the return of sea otters to Monterey Harbor, Calif., Department of Fish and Game divers made qualitative surveys of the bottom and used a garden hose to remove several clams from the substrate for identification. The bottom topography was smooth, clams were abundant, and *T. nuttallii* was the dominant species removed from as deep as 50 cm in the substrate (Ebert[3]). Follow-up survey dives soon after the return of sea otters indicated that clams were less abundant and the bottom topography was hummocky (Ebert, see footnote 3). Although definitive quantitative data are not available for that period, and although construction and dredging operations in the inner marina portion of the harbor may have had important impact on clam populations, information in the present report indicates that sea otters may have limited the abundance and distribution of *S. nuttalli* and *T. nuttallii* and that *T. nuttallii* is now only a minor species. The cause of this apparent shift in dominance from *T. nuttallii* to *S. nuttalli* is unclear. Our limited measurements of the depths of these clams in the substrate indicated that larger individuals were found deeper (to about 50 cm), but that neither

[3]E. E. Ebert, Director, Marine Culture Laboratory, California Department of Fish and Game, Granite Canyon, Coast Route, Monterey, CA 93940, pers. commun. June 1979.

species had a depth refuge from predation by sea otters, which excavated deeper than 50 cm. *Tresus nuttallii* attains larger size than *S. nuttalli* (pers. obs.), and if sea otters prefer larger clams, they may have preyed preferentially upon *T. nuttallii*. However, clams remained abundant in small areas of the harbor in spite of heavy predation by sea otters. Densities under Wharf No. 2 averaged about 17 clams/m^2; and in this area they appear to have a partial refuge from sea otters, which may have found it too difficult to dig through the debris of chunks of asphalt and clumps of barnacle tests embedded in the sediment. No such impediment to digging exists in areas A and B, where clams have persisted in somewhat lower densities of about 14 and 9/m^2, respectively. However, the species composition of clams was the same under Wharf No. 2 and in areas A and B, regardless of predation intensity.

By following tagged animals, Loughlin (1977) showed that certain sea otters made daily foraging trips to Monterey Harbor from rafting locations as far as 2 km away. In the present descriptions of their dive paths, sea otters feeding on items other than clams apparently located prey in a random manner similar to Shimek's (1977) description of an otter patting the surface of rocks and feeling the cracks. Observations of the bubble paths of otters taking clams in areas A and B of the harbor, however, indicated that they usually did not spend time searching for a suitable place to dig, nor did visual selection of a patch of clams appear to occur. If the density of clams in area A averaged 14/m^2, and if an average spot dug up by an otter was 0.5 × 1.5 m (0.75 m^2) as observed in this report, then random digging in area A would produce about 10 clams. This is greater than the average number of six clams taken by otters on a series of dives. Perhaps the otters had learned the location of the clam patches, and because sediment clouds normally prevented visual cues as soon as the substrate was disturbed, they simply dug haphazardly within the patch. Indeed, Gentry and Peterson (1967) compared the underwater visual acuity of sea otters with the sea lion, *Zalophus californianus*, and harbor seal, *Phoca vitulina*, and proposed that vision in otters may be better adapted for aerial situations of predator detection rather than for underwater prey location.

The strategy of repeatedly enlarging the hole to capture clams is a good one, because it makes efficient use of the labor to start the hole on initial dives. Anyone who has dug in sand at the seas[illegible] knows that it is relatively easy to enlarge a hole, and it would be advantageous to do this rather than dig straight down for each individual clam. The behavior of digging like a dog has also been reported by Shimek (1977) for a sea otter taking subtidal echiuroid worms and is apparently similar to the behavior of sea otters taking clams in shallow subtidal and intertidal waters in Alaska (Calkins 1978). The holes reported by these authors were only half the size of freshly dug holes at Monterey Harbor, however. The first author has observed similar (1.5 m across and 0.5 m deep) holes dug by otters in the sand channels in 12 m of water off kelp forests at Pacific Grove, Calif. In areas such as Prince William Sound and Monterey Harbor, where otters forage heavily on clams, their digging must cause a major disturbance of the infaunal community.

Sea otters have been termed "keystone predators" (Estes and Palmisano 1974; Estes et al. 1978), because they regulate populations of epibenthic invertebrates, perhaps through a process of switching between prey species. At Monterey Harbor there is circumstantial evidence that sea otters have had a major impact on two other prey items. Surveys by the California Department of Fish and Game showed *C. antennarius* and *C. productus* were taken in abundance by fishermen from the Monterey wharves prior to the return of sea otters, but they were rarely taken at Monterey in 1972-74, while still caught in abundance at piers north of the range of sea otters (California Department of Fish and Game[4]). Observations on the scuba dives reported here for 1976-77 confirm that cancer crabs are rare in the harbor. *Mytilus edulis* and *M. californianus* formed dense clumps on wharf pilings prior to the return of sea otters (Haderlie[5]), but mussels are small and uncommon there now (Haderlie and Donat 1978). Curiously, large specimens of *B. nubilus* are still abundant on the pilings and were not taken in appreciable numbers by sea otters, even though these barnacles were taken frequently by otters at other locations in the Monterey area (pers. obs.). The factors which regulate prey selection by sea otters remain poorly understood.

[4]California Department of Fish and Game. 1976. A proposal for sea otter protection and research and request for the return of management to the State of California. Calif. Dep. Fish Game, Oper. Res. Branch, Vol. 1: Text and summaries, 271 p.

[5]E. C. Haderlie, Professor, Naval Postgraduate School, Monterey, CA 93940, pers. commun. May 1976.

Acknowledgments

John S. Pearse, Ronald Jameson, and an anonymous reviewer provided advice and critical discussion for this study. Christopher Harrold gave technical and diving help. We thank the staff at Hopkins Marine Station of Stanford University for their assistance. This work was partially funded by the U.S. Fish and Wildlife Service.

Literature Cited

CALKINS, D. G.
1978. Feeding behavior and major prey species of the sea otter, *Enhydra lutris*, in Montague Strait, Prince William Sound, Alaska. Fish. Bull., U.S.76:125-131.
ESTES, J. A., AND J. F. PALMISANO.
1974. Sea otters: their role in structuring nearshore communities. Science (Wash., D.C.) 185:1058-1060.
ESTES, J. A., N. S. SMITH, AND J. F. PALMISANO.
1978. Sea otter predation and community organization in the western Aleutian Islands, Alaska. Ecology 59:822-833.
FARO, J. B.
1969. A survey of subtidal sea otter habitat off Point Pinos, California. M.A. Thesis, Humboldt State Univ., Arcata, Calif., 278 p.
GENTRY, R. L., AND R. S. PETERSON.
1967. Underwater vision of the sea otter. Nature (Lond.) 216:435-436.
HADERLIE, E. C., AND W. DONAT III.
1978. Wharf piling fauna and flora in Monterey Harbor, California. Veliger 21:45-69.
HOUK, J. L., AND J. J. GEIBEL.
1974. Observation of underwater tool use by the sea otter, *Enhydra lutris* Linnaeus. Calif. Fish Game 60:207-208.
LOUGHLIN, T. R.
1977. Activity patterns, habitat partitioning, and grooming behavior of the sea otter, *Enhydra lutris*, in California. Ph.D. Thesis, Univ. California, Los Ang., 110 p.
MCCLENEGHAN, K., AND J. A. AMES.
1976. A unique method of prey capture by a sea otter, *Enhydra lutris*. J. Mammal. 57:410-412.
RADINSKY, L. B
1968. Evolution of somatic sensory specialization in otter brains. J. Comp. Neurology 134:495-505.
SHIMEK, S. J.
1977. The underwater foraging habits of the sea otter, *Enhydra lutris*. Calif. Fish Game 63:120-122.
STEPHENSON, M. D.
1977. Sea otter predation on Pismo clams in Monterey Bay. Calif. Fish Game 63:117-120.

ANSON H. HINES

Chesapeake Bay Center for Environmental Studies
Smithsonian Institution
P.O. Box 28, Edgewater, MD 21037

THOMAS R. LOUGHLIN

Office of Marine Mammals and Endangered Species
National Marine Fisheries Service, NOAA
Washington, D C 20235

EFFECT OF ZINC ON FIN REGENERATION IN THE MUMMICHOG, *FUNDULUS HETEROCLITUS*, AND ITS INTERACTION WITH METHYLMERCURY

Methylmercury has been found to retard fin regeneration in the marsh killifish, *Fundulus confluentus*, and striped mullet, *Mugil cephalus* (Weis and Weis 1978). In *F. confluentus* the retarding effect of methylmercury was masked in water of reduced salinity (9‰). Cadmium, which also retarded fin regeneration in killifish (Weis and Weis 1976), interacted antagonistically with methylmercury so that fish exposed simultaneously to the two metals exhibited growth rates comparable to controls (Weis and Weis 1978).

This paper reports on the effects of zinc on regeneration in the mummichog, *F. heteroclitus*, and the effects of combinations of methylmercury and zinc on this process.

Methods

Fish were collected by seining in the vicinity of Montauk, N.Y. The lower portion of each caudal fin was amputated with a scalpel, and approximately 15 fish were placed in each of several all-glass aquaria with 10 l of 30‰ salinity water. The temperature was 20°-22° C and the photoperiod was 14 h light/10 h darkness. Fish were fed commerical fish food and live grass shrimp, *Palaemonetes pugio*. Tanks were dosed with methylmercuric chloride (I.C.N. Pharmaceuticals, Plainview, N.Y.[1]) from a 0.1 mg/ml stock solution in 0.2% $NaHCO_3$ to yield a final calculated concentration of 0.050 or 0.025 ppm depending on the experiment, and/or with $ZnCl_2$ (Reagent Grade, Fisher Scientific) from a 1.0 mg/ml stock solution to yield calculated concentrations of 1.0, 3.0, or 10.0 ppm. Aquaria were washed, refilled, and redosed after 2, 4, 7, 9, and 11 days. Regenerating fins were measured with a calibrated ocular micrometer in a stereomicroscope at 7, 9, 11, and 14 days. Experiments were terminated at 2 wk because after that time it became difficult to ascertain the point at which the amputation had been made. The amputation plane can be seen clearly in Figure 1, a control fin 1 wk after amputation.

Three experiments were performed. Experiment I involved exposure of fish 3.5-4.2 cm stan-

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

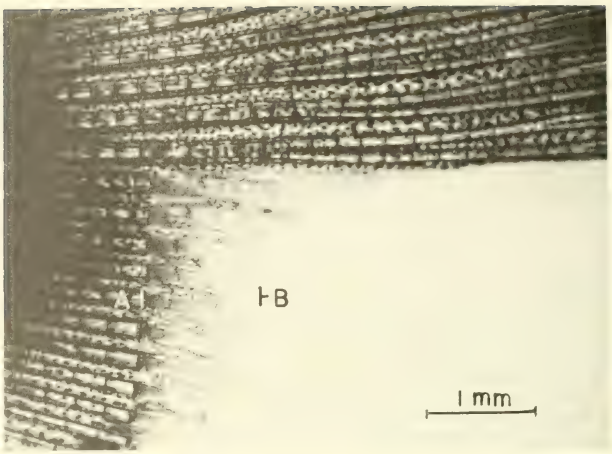


FIGURE 1.—Photograph of regenerating caudal fin, 1 wk after amputation. Measurements were made at A to B.

dard length (SL) to 0.05 ppm methylmercury, 1.0, 3.0, or 10.0 ppm zinc or combinations of 0.05 ppm methylmercury with 1.0, 3.0, or 10.0 ppm zinc. Experiment II was similar, but used 0.025 ppm methylmercury and fish 4.1-5.2 cm SL. Experiment III used 0.05 ppm methylmercury and the same concentrations of zinc, but was performed in water of reduced salinity (10‰) on fish 4.3-5.1 cm SL.

Fish were frozen at the end of some experiments and later analyzed for metal uptake by atomic absorption spectrophotometry (cold vapor technique for mercury, flameless atomic absorption spectrophotometry for zinc). These analyses can be considered accurate within 10%.

Results

In Experiment I, caudal fin regeneration was retarded by methylmercury and was accelerated by zinc in a dose-dependent fashion. The retardation produced by the mercury could be partially counteracted by the zinc (Figure 2). Analysis of variance of day 14 (Table 1) showed significant effects of mercury, and of zinc, but not of interaction.

Experiment II, using 0.025 ppm methylmercury, produced similar results (Table 2). It can be seen that zinc again accelerated growth in a dose-dependent manner and counteracted the methylmercury-caused depression of growth. Only the group in methylmercury alone and the group in 10 ppm zinc were significantly different from controls ($P \leq 0.05$) as determined by the t-test.

TABLE 1.—Analysis of variance on effects of methylmercury and zinc on fin regeneration in *Fundulus heteroclitus*.

Source of variation	df	SS	MS	F	P
Hg	1	24.778	24.778	173.671	0.001
Zn	3	2.200	0.733	5.139	0.003
Hg × Zn	3	0.411	0.137	0.960	0.416

TABLE 2.—Growth of tail regenerates in *Fundulus heteroclitus* exposed to methylmercury and zinc for 14 days in Experiment II and 11 days in Experiment III.

	Experiment II		Experiment III	
Exposure	n	mm ±SE	n	mm ±SE
Controls	12	3.62±0.078	12	2.28±0.069
meHg	15	3.31±0.128*	8	1.67±0.125*
meHg + 1 ppm Zn	12	3.59±0.099	7	1.82±0.094*
meHg + 3 ppm Zn	13	3.49±0.116	2	2.14±0.060
meHg + 10 ppm Zn	12	3.50±0.084	1	2.24±0.00
1 ppm Zn	13	3.73±0.144	11	2.43±0.098
3 ppm Zn	14	3.86±0.142	9	2.44±0.111
10 ppm Zn	10	4.18±0.159*	2	2.46±0.020*

*Significantly different from controls ($P<0.05$) by t-test.

In Experiment III (10‰ salinity) a similar pattern was seen (Table 2). High mortality due to interruption in air supply caused the experiment to be terminated early. The groups in methylmercury, methylmercury + 1 ppm zinc, and in 10 ppm zinc were significantly different from controls, as seen by the t-test.

Analysis of mercury uptake revealed considerable variation (Table 3). However, it seems likely that the tissue residues are dose dependent and that zinc does not change the uptake of mercury

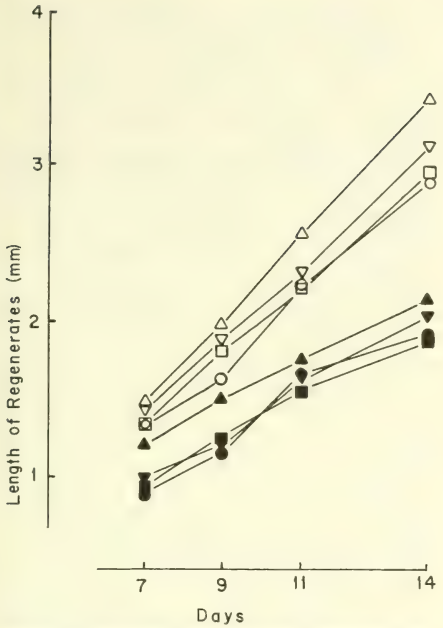


FIGURE 2.—Regenerative growth of tail fin of *Fundulus heteroclitus* exposed to methylmercury and zinc in seawater, Experiment I.
Key: △ 10.0 ppm Zn (n = 15), ▽ 3.0 ppm Zn (n = 15), □ 1.0 ppm Zn (n = 15), ○ Control (n = 14), ▲ 0.05 ppm meHg + 10.0 ppm Zn (n = 11), ▼ 0.05 ppm meHg + 3.0 ppm Zn (n = 12), ■ 0.05 ppm meHg + 1.0 ppm Zn (n = 9), ● 0.05 ppm meHg (n = 12).

TABLE 3.—Average mercury uptake (ppm Hg/wet weight ± SE) by *Fundulus heteroclitus*.

Item	Control Uptake	n	Hg Uptake	n	Hg + 10 ppm Zn Uptake	n
Experiment I:						
Carcass	n.d.[1]	3	32±5.0	3	37±7.2	3
Brain	n.d.	3	11±0.9	3	19±4.8	4
Experiment II:						
Carcass	n.d.	3	7.4±0.7	3	15.4±3.1	5
Brain	n.d.	3	4.8±2.6	3	9.7±1.6	5
Experiment III:						
Carcass	n.d.	3	33±12	3	25±1.4	3
Brain	n.d.	3	28±6.0	3	25±2.5	3

[1]n.d. = not detectable, <0.03 ppm.

into the brain or the rest of the body. Accumulation of zinc was not altered by methylmercury. Animals in 10 ppm Zn accumulated 246±1.41 ppm; those in 10 ppm Zn + 0.05 ppm meHg accumulated 250±3.54 ppm. Those in 1 and 3 ppm Zn accumulated 221±25.2 and 250±4.95 ppm, showing no clear dose-dependent relationship.

Discussion

The data indicate that in *F. heteroclitus*, zinc can accelerate regenerative growth, and, by so doing, can counteract the retarding effects of methylmercury. In this species, the regeneration rate of controls was similar in 30‰ and 10‰ salinity, and the methylmercury retarded growth at both salinities. This is in contrast to *F. confluentus* in which decreased salinities depressed the regeneration rate, thus masking the effects of methylmercury in water of 9‰ salinity (Weis and Weis 1978).

Methylmercury has previously been observed to retard regeneration (Chang et al. 1976; Weis and Weis 1978) and other developmental processes (Chang et al. 1974). Its action as an inhibitor of mitosis (Ramel 1969) could be the cause of these effects on growth processes. As a potent nerve poison it could further inhibit regenerative growth by interfering with the neurotrophic influence necessary for regeneration.

Previous studies on the effects of zinc on growth include the work of Hirsch and Hurley (1978) in which zinc was found to counteract the teratogenic effects of 6-mercaptopurine in the rat. They felt that the drug lowered DNA synthesis and that the zinc counteracted this. Swenerton et al. (1969) correlated zinc deficiency with reduced DNA synthesis in rat embryos, and Falchuck et al. (1975) have associated zinc with promoting cell division in *Euglena gracilis*. Thus, if zinc can promote DNA synthesis and cell division in fish also, that would account for the observed acceleration of regenerative growth. However, previous studies on fish have not indicated such an effect. Crandall and Goodnight (1962) reported that 1.15 ppm zinc retarded the growth of newborn guppies. Rachlin and Perlmutter (1969) found that 18 ppm Zn reduced the mitotic index of cultured rainbow trout, *Salmo gairdneri*, cells, but that 1.8-10.0 ppm had no effect on the mitotic index.

On the other hand, zinc has often been found to counteract toxic effects of other heavy metals. Dixon and Compher (1977) found that zinc could reverse a cadmium-caused inhibition of regeneration in the newt. Zinc has been found to counteract the toxic effects of mercury in rats (Yamane et al. 1977) and to counteract the teratological effects of methylmercury in killifish embryos (Weis et al. in press).

In view of reports of fin rot of unknown etiology in flatfish from polluted environments (Ziskowski

and Murchelano 1975), the retardation of growth by heavy metals may be of significance in inhibiting regeneration of fins eroded by the benthic substrate.

Addendum

It has recently been demonstrated that, in certain poeciliid fishes, some environmental variables which affect general growth rate do not affect the rate of fin regeneration. Factors which do cause differences in length of regenerated fin generally affect the time needed for wound healing and blastema formation, rather than rates of regeneration per se (E. Zimmerer, Ph.D. dissertation, Rutgers University, 1980). We tested the data represented in Figure 1 for this possibility. In regression analysis, the slope equals regenerative rate per se and the elevation (y-intercept) represents the time needed for wound healing and blastema formation. Analysis of covariance indicates that when Hg treated fish are compared with control fish, both the slopes and y-intercepts are significantly different (F = 10.23 and 80.76, respectively). Similarly, when 10 ppm Zn treated and control fish are compared, the slopes and y-intercepts are significantly different (F = 6.83 and 41.29, respectively). Therefore, it appears that these heavy metals affect both the initial wound healing and blastema formation and the rate of regeneration per se.

Acknowledgments

This work is a result of research sponsored by NOAA Office of Sea Grant, U.S. Department of Commerce, under grant No. 04-7-158-44042. Thanks are extended to J. C. Baiardi of the New York Ocean Science Laboratory for the use of facilities for this study, and to J. Seebode Jr., J. Ricci, and G. Millinger for technical assistance. We thank S. L. Cheng of the New Jersey Institute of Technology for the atomic absorption spectrophotometry, and J. Chou of the College of Medicine and Dentistry of New Jersey for statistical assistance.

Literature Cited

CHANG, L. W., L. M. MAK, AND A. H. MARTIN.
1976. Dose-dependent effects of methylmercury on limb regeneration of newts (*Triturus viridescens*). Environ. Res. 11:305-309.

CHANG, L. W., K. R. REUHL, AND A. W. DUDLEY, JR.
1974. Effects of methylmercury chloride on *Rana pipiens* tadpoles. Environ. Res. 8:82-91.

CRANDALL, C. A., AND C. J. GOODNIGHT.
1962. Effects of sublethal concentrations of several toxicants on growth of the common guppy, *Lebistes reticulatus*. Limnol. Oceanogr. 7:233-239.

DIXON, C., AND K. COMPHER.
1977. The protective action of zinc against the deleterious effects of cadmium in the regenerating forelimb of the adult newt, *Notophthalmus viridescens*. Growth 41:95-103.

FALCHUCK, K. H., D. W. FAWCETT, AND B. L. VALLEE.
1975. Role of zinc in cell division of *Euglena gracilis*. J. Cell Sci. 17:57-78.

HIRSCH, K. S., AND L. S. HURLEY.
1978. Relationship of dietary zinc to 6-mercaptopurine teratogenesis and DNA metabolism in the rat. Teratology 17:303-314.

RACHLIN, J. W., AND A. PERLMUTTER.
1969. Response of rainbow trout cells in culture to selected concentrations of zinc sulfate. Prog. Fish-Cult. 31:94-98.

RAMEL, C.
1969. Genetic effects of organic mercury compounds. I. Cytological investigations on *Allium* roots. Hereditas 61:208-230.

SWENERTON, H., R. SHRADER, AND L. S. HURLEY.
1969. Zinc-deficient embryos: reduced thymidine incorporation. Science (Wash., D.C.) 166:1014-1015.

WEIS, J. S., P. WEIS, AND J. L. RICCI.
In press. Effects of cadmium, zinc, temperature, and salinity on the teratogenicity of methylmercury to the killifish, *Fundulus heteroclitus*. *In* Second International Symposium on the Early Life History of Fishes, sponsored by International Council for the Exploration of the Seas, Woods Hole, Mass., April 2-5, 1979.

WEIS, P., AND J. S. WEIS.
1976. Effects of heavy metals on fin regeneration in the killifish, *Fundulus heteroclitus*. Bull. Environ. Contam. Toxicol. 16:197-202.
1978. Methylmercury inhibition of fin regeneration in fishes and its interaction with salinity and cadmium. Estuarine Coastal Mar. Sci. 6:327-334.

YAMANE, Y., H. FUKINO, AND M. IMAGAWA.
1977. Suppressive effect of zinc on the toxicity of mercury. Chem. Pharm. Bull. (Tokyo) 25:1509-1518.

ZISKOWSKI, J., AND R. MURCHELANO.
1975. Fin erosion in winter flounder (*Pseudopleuronectes americanus*) from the New York Bight. Mar. Pollut. Bull. 6:26-28.

PEDDRICK WEIS

Department of Anatomy
New Jersey Medical School
Newark, NJ 07103

JUDITH SHULMAN WEIS

Department of Zoology and Physiology
Rutgers, the State University
Newark, NJ 07102

SOUTHERN DISTRIBUTION OF THE ATLANTIC WHITESIDED DOLPHIN, *LAGENORHYNCHUS ACUTUS*, IN THE WESTERN NORTH ATLANTIC

Two mass strandings of the Atlantic whitesided dolphin, *Lagenorhynchus acutus*, in New England—Wellfleet, Mass., 11 May 1973 and Edmunds, Maine, 6 September 1974—initiated investigation at the New England Aquarium, Boston, into this species' life history and pathobiology. Previous distribution records for this species in the United States were reported by Cope (1876), True (1885, 1889), and Schevill (1956). Most references define this dolphin's southern distribution as Cape Cod, Mass. We believe this is based on a 206 cm female reported to have been collected near Portland, Maine, and described by Cope (1876) as *L. perspicillatus* (= *L. acutus*). Norton (1930) redescribed the correct collecting site as Cape Cod.

The first confirmed Cape Cod report, although not a stranding, was on 14 September 1954 when a school sighting and harpooned specimen were reported by Schevill (1956). This school, about 12 animals, was located 93 km east of Cape Cod in water 145 m deep (Figure 1, number 3).

The following accounts, arranged in chronological order, update our present knowledge of this species' southernmost known occurrence in the western North Atlantic. Information is based upon stranding records of the Smithsonian Institution and the New England Aquarium, along with an examination of the collections of the American Museum of Natural History, New York, N.Y.; Academy of Natural Sciences, Philadelphia, Pa.; U.S. National Museum, Washington, D.C.; and the Museum of Comparative Zoology, Harvard University, Cambridge, Mass. Paragraph numbers below correspond to locality numbers in Figure 1 and to reported body measurements given in Table 1. Abbreviations for collection numbers are as follows: MCZ = Museum of Comparative Zoology, Harvard University, NEA = New England Aquarium, USNM = U.S. National Museum.

1. One male (USNM 22934) captured by the U.S. Fisheries schooner *Grampus* 20 mi (37 km) south of Montauk, Long Island, N.Y. (lat. 40°38′ N, long. 71°49′ W), 19 May 1888. This specimen was reported to have been captured from a school of about 100 animals.

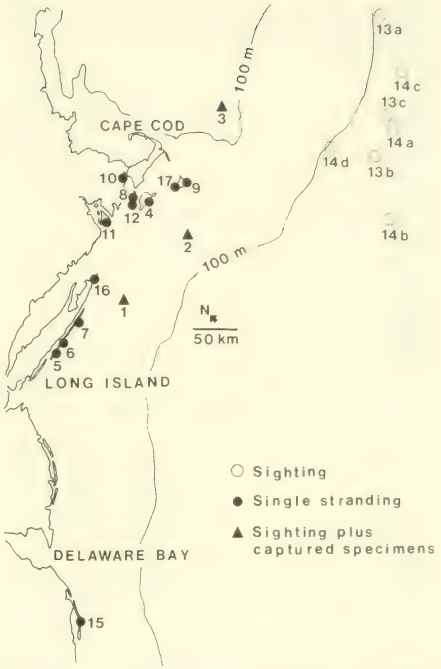


FIGURE 1.—Southernmost east coast locations of known Atlantic whitesided dolphin sightings. Numbers refer to specimens described in Table 1 and in text.

2. One female (USNM 22942), also captured by the *Grampus*, taken south of Cape Cod Islands (lat. 40°43′ N, long. 70°32′ W). No date recorded but because of its proximity to the prior animal's catalog number, we believe this animal was taken on the same cruise.

3. One female (MCZ 48548) harpooned from a small school off Cape Cod (lat. 41°35′ N, long. 68°55′ W), 14 September 1954 (Schevill 1956).

4. One skull (MCZ 48549) collected during the winter 1954-55 at South Beach, Martha's Vineyard, Mass.

5. One specimen washed ashore live at Ocean Beach, Fire Island, Long Island (lat. 40°39′ N, long. 73°09′ W), April 1971. Length estimated at about 7.5 ft (229 cm), sex undetermined. Skull measurements: condylobasal length, 391 mm; rostrum length, 196 mm; tooth width, up to 4 mm; dental formula $\frac{33-}{34-34}$.

TABLE 1.—Selected body measurements, nearest whole centimeter, of *Lagenorhynchus acutus* from the southernmost known occurrences in the western North Atlantic. Data in parentheses converted from English to metric. Doubtful measurements were not included. Localities are given in Figure 1 and text.

Measurement	Locality number and sex								Range	Percentage of total length	
	1(M)	2(F)	3(F)	7(M)	9(F)	10(F)	11(M)	12(-)		Range	Mean
Snout to:											
Notch, total length	(150)	(209)	225	233	165	224	202	(241)	150-241	—	—
Flipper	—	(38)	40	32	18	35	30	(41)	18-41	10.9-18.2	15.4
Tip of dorsal fin	—	—	87	88	93	119	112	—	87-119	37.8-56.4	48.3
Genital slit	—	(137)	—	153	112	157	125	(173)	112-173	61.9-71.8	67.2
Anus	(109)	—	—	—	118	165	141	(182)	109-182	69.8-75.5	72.6
Apex of melon	—	—	4	5	3	5	5	—	3-5	1.8-2.5	2.1
Center of eye	(22)	—	—	28	22	25	24	—	22-28	11.2-14.7	12.6
Angle of mouth	(19)	(25)	—	23	17	21	20	—	17-25	9.4-12.7	10.7
Ear	—	—	—	37	16	33	29	—	16-37	9.7-15.9	13.7
Girth:											
Maximum	—	—	—	103	91	119	121	—	91-121	43.8-59.9	53.0
At axilla	—	—	—	85	84	106	108	—	84-108	42.1-53.5	48.4
At eye	—	—	—	82	68	80	80	—	68-82	35.2-41.2	37.9
Flipper lengths:											
Anterior	(24)	(32)	—	34	25	34	28	(36)	24-36	13.9-15.3	15.0
Posterior	—	—	25	23	16	25	20	(24)	16-25	9.7-11.2	10.3
Maximum flipper width	(8)	(12)	—	14	9	12	11	(13)	8-14	5.3-6.0	5.5
Dorsal fin height	(15)	(22)	24	—	12	25	18	(22)	12-25	7.3-10.7	9.7
Fluke width	(35)	(57)	65	55	36	55	43	—	35-65	21.3-28.9	24.4
Number of visible teeth	—	—	30-30 31-32	30-30 30-30	31-29 32-31	—	30-32 30-30	33-30 32-31	—	—	—

6. One specimen, length and sex unknown, found along Patchogue, Long Island (lat. 40°43′ N, long. 72°57′ W), December 1973. Only the head and the tail were recovered. Estimation of total length from photographs is 160 cm. Tooth count from visible teeth was $\frac{-25}{-31}$.

7. One dead male found in surf line at Village Beach, Village of Westhampton Beach, Long Island (lat. 40°48′ N, long. 72°38′ W), 1 May 1974. Currently, the skeleton is on display at the New York Ocean Science Laboratory, Montauk, Long Island.

8. Decayed carcass of a 150 cm individual (skull USNM 504292), sex indeterminate, was examined on the southeastern corner of Pasque Island, Mass., Nantucket Sound (lat. 41°26′ N, long. 70°51′ W), 5 July 1975. According to residents, this animal had stranded 2 or 3 mo earlier thereby placing the stranding date in April or May.

9. A female (NEA MH7622) found live and later died on the southern side of Nantucket Island, Mass. (lat. 40°14′ N, long. 70°00′ W), 15 February 1976.

10. A female (NEA MH7670), 127.6 kg, stranded alive and later died at Marion, Mass. (lat. 41°42′ N, long. 70°46′ W), 28 April 1976.

11. One dead male (NEA MH7672), 109 kg, found on the eastern edge of Easten's Beach, Newport, R.I. (lat. 41°29′ N, long. 71°17′ W), 1 May 1976.

12. One decayed specimen (NEA MH76129), sex unknown, thought to have stranded during spring 1976. Found early May on the outer side of Cuttyhunk Island, Nantucket Sound, Mass. (lat. 41°25′ N, long. 70°56′ W).

13. Three 1976 sightings reported southeast of Cape Cod along the southeast edge of Georges Bank by the NOAA Ship *Albatross IV*, fall survey 76-09:

a. School of 15-20 animals, lat. 41°13′ N, long. 66°15′ W, 27 March.
b. Two animals, lat. 40°10′ N, long. 67°12′ W, 2 April.
c. Five animals, lat. 40°26′ N, long. 67°03′ W, 2 August.

14. Four sightings on 2 January 1977 during U.S. Coast Guard aerial overflights during the *Argo Merchant* Oil Spill (Grose and Mattson[1]):

a. Two animals, lat. 40°21′ N, long. 66°58′ W.
b. One animal, lat. 39°29′ N, long. 68°20′ W.
c. One animal, lat. 40°34′ N, long. 66°36′ W.
d. One animal, lat. 40°30′ N, long. 68°03′ W.

15. One female, 248 cm, stranded dead about 2.4 km south of the Virginia-Maryland border on Chincoteague National Wildlife Refuge in Virginia (lat. 38°02′ N, long. 75°18′ W), 27 May 1977.

16. A freshly stranded male animal, 234 cm, found at Deerfield Lane Beach, Amagonsett, Long

[1]Grose, P. L., and J. S. Mattson. 1977. The ARGO MERCHANT Oil Spill—A preliminary scientific report. U.S. Department of Commerce, Washington, D.C., Special Report, 323 p.

Island (lat. 41°00′ N, long. 72°05′ W), 30 August 1978.

17. On Nantucket Island, Eel Point (lat. 41°17′ N, long. 70°05′ W), approximately 200 cm specimen (NEA MH78143), sex unknown. The stranding took place on 4 September 1978.

The Virginia stranding extends the southern distribution approximately 700 km southwest of Schevill's (1956) sighting. These reportings south of lat. 41° N indicate that the range of the Atlantic whitesided dolphin is farther south than the Cape Cod area thus extending the range into the Middle Atlantic Bight.

There were two previous published records which had placed this species farther south than Schevill's reporting; however, these appear to be erroneous. True (1885) reported a series of skulls of *L. perspicillatus* (= *L. acutus*) taken in a net fishery at Fort Macon, N.C. That collection of skulls, now in the USNM, were examined and determined to be bottlenosed dolphin, *Tursiops truncatus* (Mead 1975). Rhoads (1903) listed *L. acutus* as possibly occurring off the coast of New Jersey based upon an illustration in Godman (1828). An examination of the original illustration indicates that the species depicted was a common dolphin, *Delphinus delphis*.

These occurrences, as far south as the Chesapeake Bight, indicate the southernmost known extent of the Atlantic whitesided dolphin distribution along the western North Atlantic. It appears from this information that the Atlantic whitesided dolphin has a peak occurrence in the Mid-Atlantic Region during spring and summer.

This work was supported in part by the U.S. Marine Mammal Commission, Contract Number MM5AC008 with the New England Aquarium.

Acknowledgments

The authors wish to express their gratitude to W. E. Schevill, Woods Hole Oceanographic Institution, for stranding data from the MCZ. We especially thank P. Connor, New York State Museum, and A. Cooley, Bellport High School, Bellport, Long Island, N.Y., for their contributions of Long Island stranding information. We thank E. E. Britton, Chincoteague National Wildlife Refuge for the information of the Virginia stranding and G. K. Mahoney, Fisheries Management Division, NMFS, NOAA, for his constructive criticism.

Literature Cited

COPE, E. D.
1876. Fourth contribution to the history of the existing Ceatacea. Proc. Acad. Nat. Sci. Phila., Ser. 3, 28:129-139.

GODMAN, J. J.
1828. American natural history. Vol. III, Part 1, Mastology. Carey, Lea and Carey, Phila., 264 p.

MEAD, J. G.
1975. Preliminary report on the former fisheries for *Tursiops truncatus* in the western North Atlantic. J. Fish. Res. Board Can. 32:1155-1162.

NORTON, A. H.
1930. The mammals of Portland, Maine, and vicinity. Proc. Portland Soc. Nat. Hist. 4, 155 p.

RHOADS, S. N.
1903. The mammals of Pennsylvania and New Jersey. Privately published, Phila., 206 p.

SCHEVILL, W. E.
1956. *Lagenorhynchus acutus* off Cape Cod. J. Mammal. 37:128-129.

TRUE, F. W.
1885. The porpoise fishery of Hatteras, N.C. Bull. U.S. Fish. Comm. 5:3-6.
1889. A review of the Family Delphinidae. Bull. U.S. Natl. Mus. 36, 191 p.

SALVATORE A. TESTAVERDE

New England Aquarium
Boston, Mass.
Present address: *Fisheries Management Division*
National Marine Fisheries Service, NOAA
State Fish Pier, Gloucester, MA 01930

JAMES G. MEAD

Division of Marine Mammals
Smithsonian Institution
Washington, DC 20560

ADDITIONAL RECORDS OF THE SCULPIN *PSYCHROLUTES PHRICTUS* IN THE EASTERN BERING SEA AND OFF OREGON

Psychrolutes phrictus Stein and Bond is an unusually large *Psychrolutes* known heretofore from deep water between Monterey, Calif., and northern Oregon. The species can be distinguished from its only congener, *P. paradoxus*, by differences in relative head length, gill raker and pectoral fin ray counts, and the presence of small cirri on both head and body. Recent collections in the Bering Sea and off Oregon supplement the type-description and contribute new information on range and early life history.

During a 2-mo period (summer 1978), while a member of the foreign fisheries observer staff of

the National Marine Fisheries Service, Colin Lau[1] subsampled trawl catches northwest of Unalaska Island on the Japanese fishing vessels *Tomi Maru No. 53* and *Eikyu Maru No. 12*. Lau often noticed a cottidlike fish that he was unable to identify with certainty. Two specimens of this fish, which he preserved, were accessed into the University of Washington fish collection and later identified by the authors as *P. phrictus*. Collection data for the two specimens (UW 20762 and 20763) and for two pelagic juveniles (OSUO 2437 and 2438), obtained in an opening-closing midwater trawl off Oregon (Pearcy et al. 1977), are given in Table 1.

[1]Colin Lau, College of Fisheries, University of Washington, Seattle, WA 98195, pers. commun. October 1978.

Confirmation of the identity of these four specimens was made by comparisons with the meristic and morphometric characters used in the original description (Table 2). Methods for counting and measuring are as in Hubbs and Lagler (1964); measurements were taken to the nearest 0.1 mm with dial calipers; unpaired fin rays and vertebrae were counted on radiographs. These specimens were slightly different from those previously available. The larger specimen from the Bering Sea (UW 20763) has an additional caudal vertebra that may have resulted from development in colder waters. The two juveniles from off Oregon have relatively larger heads than reported previously—evidence of the allometry described by Stein and Bond (1978).

TABLE 1.—Collection data for *Psychrolutes phrictus* in the eastern Bering Sea and off Oregon, 1978.

Specimen source	Date	Position		Haul depth (m)	*Psychrolutes phrictus*		Subsample weight (kg)
		Lat. N	Long. W		Number	Weight (kg)	
Tomi Maru No. 53	19 June	54°31′	167°35′	790	1	—	—
	25 June	54°29′	167°25′	685	1	—	—
	25 June	54°26′	167°30′	740	1	—	—
	26 June	54°41′	167°32′	680	1	—	—
	26 June	54°38′	167°29′	660	[2]1	—	—
	2 July	54°20′	167°22′	900	1	—	—
Eikyu Maru No. 12	13 July	54°22′	166°55′	868	1	5.0	94.7
	20 July	54°18′	167°08′	1,240	1	3.5	118.2
	21 July	54°21′	166°50′	925	1	7.7	135.2
	22 July	54°20′	166°53′	1,050	1	5.4	131.1
	22 July	54°20′	166°51′	940	1	8.0	119.2
	25 July	54°20′	166°52′	850	[2]1	0.3	96.0
	26 July	54°19′	166°52′	925	4	11.4	139.1
	26 July	54°15′	167°07′	1,320	1	4.6	133.3
	28 July	54°22′	166°55′	865	1	7.9	132.2
OSUO[3] 2437	1 Sept.	44°47′	125°50′	495-505	1	—	—
OSUO 2438	2 Sept.	44°37′	125°43′	480-540	1	—	—

[1]University of Washington (UW) collection, Seattle, Wash.; [preserved] specimen UW 20762.
[2][Preserved] specimen UW 20763.
[3]Oregon State University Oceanography (OSUO) collection, Corvallis, Oreg.

TABLE 2.—Meristic and morphometric (measurement in millimeters and percentage within parentheses) characters of *Psychrolutes phrictus* from the eastern Bering Sea and off Oregon.

Item	UW 20762	UW 20763	OSUO 2438	OSUO 2437	Stein and Bond (1978)[1]
Standard length, mm	113	126	28	30	
Fin rays:					
Dorsal	VIII, 20	VIII, 20	VIII, 19 or 20	VIII, 19	VII-IX, 19-20
Anal	13	13	13	13	12-14
Pectoral	23	23	24	23	22-26
Pelvic	I, 3	I, 3	I, 3	I, 3	I, 3
Principal caudal	11	11	11	11	About 13
Gill rakers	11	9	[2]9	[2]9	9-13
Vertebrae:					
Total vertebrae	35	36	34	35	33-35
Precaudal	12	12	13	13	—
Caudal	23	24	21	22	—
Head length[3]	46.4(41)	65.7(52)	15.9(55)	15.3(48)	(43.5-60.6)
Eye length[4]	9.6(21)	9.9(15)	3.2(20)	3.4(22)	(8.6-24.3)
Pectoral fin length[4]	30.2(65)	34.1(52)	7.6(48)	8.0(52)	(44.9-62.3)
Pelvic fin length[4]	10.2(22)	20.3(31)	4.0(25)	4.8(31)	(23.3-34.7)
Preanal length[4]	59.8(129)	75.1(114)	15.4(97)	12.7(83)	(93.8-132.2)

[1]Ranges for data in the original description.
[2]May be incomplete.
[3]Percentage is proportion of standard length.
[4]Percentage is proportion of head length.

Lau's observations on relative abundance of *P. phrictus* indicate that this species may constitute a significant portion of the demersal fish biomass in the area of the Bering Sea where he sampled. During a sampling period from 12 to 31 July, 76 hauls were taken, of which 38 were subsampled. *Psychrolutes phrictus* was present in subsamples from 9 of these 38 hauls and ranked 6 of 44 species found, based on weight. When individuals were present in subsamples of the catch, they represented 0.3-8.2% of the subsample weight (Table 1) and 1.8% of the overall subsample weight for the sampling period. Individuals were also observed casually in hauls where they were not part of the subsample.

The capture of two juveniles off the Oregon coast about 2,500 m above the bottom and about 65 km west of the lower continental slope is evidence that the larvae and juveniles are pelagic. Whether juveniles normally occur so far offshore, and if so, whether such individuals survive to reach the bottom, is not known. *Psychrolutes phrictus* probably leaves the pelagic zone and becomes demersal at about 30 mm. The rationale for this is that the juveniles (28 and 30 mm) reported here were pelagic, whereas those (30 and 49 mm) reported by Stein and Bond (1978) were benthic.

Literature Cited

HUBBS, C. L., AND K. F. LAGLER.
1964. Fishes of the Great Lakes Region. Revised ed. Univ. Mich. Press, Ann Arbor, Mich., 213 p.

PEARCY, W. G., E. E. KRYGIER, R. MESECAR, AND F. RAMSEY.
1977. Vertical distribution and migration of oceanic micronekton off Oregon. Deep-Sea Res. 24:223-245.

STEIN, D. L., AND C. E. BOND.
1978. A new deep-sea fish from the eastern North Pacific, *Psychrolutes phrictus* (Pisces: Cottidae [Psychrolutinae]). Nat. Hist. Mus. Los Ang. Cty., Contrib. Sci. 296, 9 p.

ANN C. MATARESE

Northwest and Alaska Fisheries Center
National Marine Fisheries Service, NOAA
2725 Montlake Boulevard East
Seattle, WA 98112

DAVID L. STEIN

School of Oceanography
Oregon State University
Corvallis, OR 97331

A RECURRENT MASS STRANDING OF THE FALSE KILLER WHALE, *PSEUDORCA CRASSIDENS*, IN FLORIDA

The false killer whale, *Pseudorca crassidens*, is one of the several species of odontocetes known primarily through its relatively frequent mass strandings. These strandings offer a large amount of natural history data but, in most cases, investigators have been unable, for various reasons, to thoroughly study these events. As a result, very few data are available on the natural history of *P. crassidens* (Mitchell 1975a, b; Purves and Pilleri 1978). *Pseudorca crassidens* is distributed worldwide in temperate and tropical waters (Mitchell 1975b), and frequently strands in large numbers (Norman and Fraser 1948; Dudok van Heel 1962), exceeding 800 in one case (Marelli 1953; Tomilin 1957; Reiger 1975). The series of *P. crassidens* mass strandings we describe herein is the third in Florida in recent years. Caldwell et al. (1970) reported a stranding of 150-175 false killer whales near Ft. Pierce on the Atlantic coast of Florida in January 1970. Little data was collected and most of the animals were apparently buried on the beach. A heretofore unreported stranding occurred on 18-19 July 1972 on the northeast end of Sawyer Key (lat. 24°45.6′ N, long. 81°33.4′ W) in the lower Florida Keys on the Florida Bay (Gulf of Mexico) side. This site is approximately 35 km northeast of Key West (Figure 1). Nineteen animals were involved. Gordon Hubbell[1] estimated the largest animals to be 460 cm (15 ft) long. He measured a 320 cm (10.5 ft) male, a 376 cm (10.3 ft) female, and a 427 cm (14.0 ft) female.

Sequence of Events

1. The Florida Marine Patrol[2] reported a whale stranding near North Captiva Island on the southwest coast of Florida (Figure 1) on the morning of 22 July 1976. We found a dead 440 cm female false killer whale at Redfish Pass (Figure 2) and four live females aground on a sandbar in Pine Island Sound (Figure 2). We necropsied the dead animal on the beach and transported the live animals to Sea World, Orlando, Fla., on 22 July. At least 29 false killer whales had entered Pine Island Sound: 1 died; 4 were stranded alive; 24

[1]Gordon Hubbell, Director, Crandon Park Zoo, Miami, Fla. 33149, pers. commun. 1977.
[2]Florida Marine Patrol, Officer in Charge, Ft. Myers Office, pers. commun. July 1976.

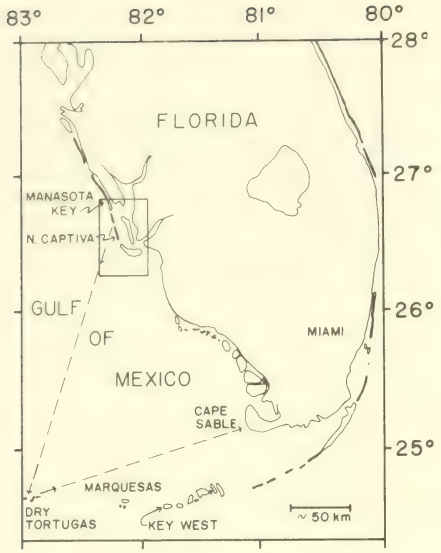


FIGURE 1.—Outline map of south Florida indicating principal stranding sites and possible routes of travel of the false killer whale herd. Fort Pierce is located just north of lat. 27° N on the east coast of the state. Box represents region covered by succeeding figure.

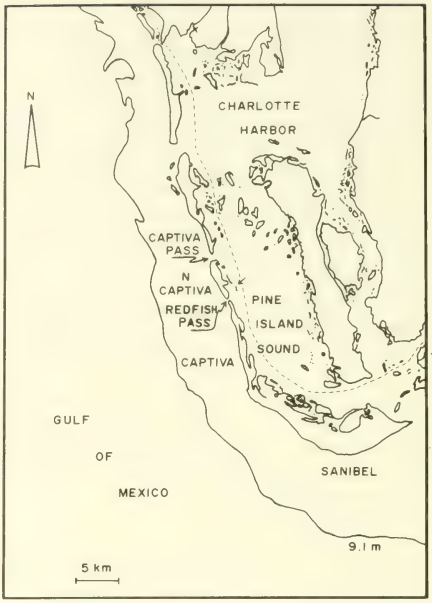


FIGURE 2.—North Captiva Island and vicinity, south Florida, indicating Redfish Pass and Captiva Pass where the false killer whales entered and exited Pine Island Sound. The four females taken to Sea World stranded on a sand bar located off the southeast side of North Captiva (indicated by an arrow). Intracoastal waterway is indicated by dashed line in Charlotte Harbor and Pine Island Sound.

were photographed exiting Captiva Pass (Larson[3]). All moved northward in or near the Intracoastal Waterway after entering Pine Island Sound via Redfish Pass. They continued northward and returned to the Gulf of Mexico via Captiva Pass (Florida Marine Patrol see footnote 2; Larson see footnote 3) (Figure 2). The animals originally entered Redfish Pass at about 0830 h. The tide was rising and near the high point (Florida Marine Patrol see footnote 2). The exact time, and thus tidal conditions when the animals exited Captiva Pass are unknown to us. It is interesting to note that a spinner dolphin, *Stenella longirostris*, herd stranded on Casey Key (lat. 27°12′10″ N, long. 82°30′30″ W) 7 days earlier (Mead et al.[4]). This site is about 75 km north of North Captiva.

2. A herd of 30 false killer whales stranded on Loggerhead Key, Dry Tortugas (Figure 1), at approximately 1300 h on 25 July on a falling tide. This site is some 235 km south of North Captiva Island. The herd was divided into two groups at the time of stranding (Shinn[5]). The animals were pushed back into the water and kept wet by U.S. Coast Guard and National Park Service personnel. We measured and sexed the animals and photographed their dorsal fins and flukes for individual identification of the animals on 26 July. We repeated the measurements and photographs, collected blood samples and marked each animal with a spaghetti tag (Floy Tag FD-68B[6] anchor

[3]Peter Larson, *Sanibel Island Reporter*, Sanibel, Fla., pers. commun. 1976.

[4]Mead, J. G., D. K. Odell, R. S. Wells, and M. Scott. 1978. Biological observations on a mass stranding of spinner dolphins (*Stenella longirostris*) from the west coast of Florida. Unpubl. manuscr. Division of Mammals, Smithsonian Institution, Washington, DC 20560.

[5]Eugene Shinn, U.S. Geological Survey, Miami, Fla., pers. commun. 1976.

[6]Floy Tag & Manufacturing Inc., Seattle, Wash. Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

tag) on 27 July. A 520 cm male died prior to an attempt to return all of the animals to offshore waters. A group effort by Park Service, Florida Marine Patrol, Coast Guard, and other personnel successfully forced the remaining 29 out to sea. Color photographs and a popular description of this stranding are given by Porter (1977).

3. On 2 August, National Park Service personnel found three shark-eaten *P. crassidens* carcasses floating about 2 km off Cape Sable (Figure 1). They towed these to shore and Odell examined them on 3 August.

4. On 23 August, Odell salvaged 20 *P. crassidens* skulls from carcasses discovered on Cape Sable by the National Park Service on 18 August. The whales were severely decomposed when first discovered and had probably been on the beach for at least 2 wk. Sex determination and external measurements were not possible (Odell and Asper[7]; Odell et al.[8]).

Results and Discussion

We measured 29 of the 30 whales that stranded on Loggerhead Key (total length only). The mean length (±SD) of 12 males was 458±48 cm, range 377-534 cm and 17 females was 416±39 cm, range 328-494 cm. The mean lengths were significantly different at the 0.01 level. The weight-length data (250 kg, 297 cm; 327 kg, 338 cm; 359 kg, 358 cm; 773 kg, 475 cm) from the four live females that we collected at North Captiva Island yielded the following predictive allometric equation corrected for log transformation bias (Beauchamp and Olson 1973): $W = 2.16 \times 10^{-4} L^{2.437}$, where W is weight in kilograms and L is length in centimeters.

The length exponent in the above equation is low when compared with similar equations for several other marine mammals. Bryden (1972) summarized the weight-length relationships for a number of marine mammals. The length exponents for several cetaceans are: *Delphinapterus leucas*—two populations, males, 2.536 and 2.605 (Sergeant and Brodie 1969); *Globicephala melaena*—2.895; *Balaenoptera musculus*—3.25 (Ash 1952); *B. physalus*—2.9 (Ash 1952); *B. borealis*—two populations, 2.43 and 2.74 (Omura 1950; Fujino 1955); and *Megaptera novaeangliae*—3.1 (Ash 1953). The mean (±SD) of these eight length exponents is 2.807±0.283. The relatively low length exponent for *P. crassidens* could be due to the small sample size or perhaps to poor condition of the animals, since we do not know how long the animals had been without food before stranding. However, the 95% confidence limits on the *P. crassidens* length exponent are 2.437±0.564.

The necropsies of six (four captive, two in field) recently decreased whales indicated extensive parasitism. Most apparent in all animals were hundreds (perhaps thousands) of the acanthocephalan worm, *Bolbosoma capitatum*, attached to the walls of the small intestine (Overstreet[9]). We found pieces of intestine with attached acanthocephalans near the Cape Sable animals. Five of the six animals had hundreds of the nematode, *Stenurus globicephalus*, in the pterygoid sinus complex. Three animals had the stomach nematode, *Anisakis* cf. *simplex* (Overstreet see footnote 9). Four animals had *S. globicephalus* in the lungs (Overstreet see footnote 9). Notable was the apparent absence in all six animals of cestode plerocercoid cysts in the blubber. Histopathology revealed that the ultimate cause of death of the four captive females was primarily pneumonia with some parasitic involvement.[10] The pathological condition(s) that led to pneumonia remain speculative. Hall and Schimpff[11, 12] examined the brains of the captive animals and of the male that died on Loggerhead Key and found them free of major neurologic disease, although they stated that some animals exhibited "behavioral symptoms suggestive of

[7]Odell, D., and E. Asper. 1977. A summary of information derived from a mass stranding of *P. crassidens* in Florida, 1976. (Abstr.) Marine Mammal Stranding Workshop, Athens, Ga., 10-12 August, 1977, p. 20-21. U.S. Marine Mammal Commission contract MM7AC020.

[8]Odell, D. K., E. D. Asper, J. Baucom, and L. H. Cornell. 1979. A summary of information derived from the recurrent mass stranding of a herd of false killer whales, *Pseudorca crassidens* (Cetacea: Delphinidae). *In* J. R. Geraci and D. J. St. Aubin (editors), Biology of marine mammals: insights through strandings, p. 207-222. Final Rep., U.S. Marine Mammal Commission contract MM7AC020. Available Natl. Tech. Inf. Serv., Springfield, Va., as PB 293380.

[9]Robin Overstreet, Gulf Coast Research Laboratory, Ocean Springs, MS 39564, pers. commun. September 1976.

[10]Armed Forces Institute of Pathology, Washington, DC 20306, cases 1579706 and 1579707, pers. commun. October 1976.

[11]Hall, N. R., and R. D. Schimpff. 1977. Neuropathology in relation to stranding. 2. Mass stranded whales. (Abstr.) Marine Mammal Stranding Workshop, Athens, Ga., 10-12 August 1977, p. 28-29. U.S. Marine Mammal Commission contract MM7AC020.

[12]Hall, N. R., and R. D. Schimpff. 1979. Neuropathology in relation to strandings: mass strandings. *In* J. R. Geraci and D. J. St. Aubin (editors), Biology of marine mammals: insights through strandings, p. 236-242. Final Rep., U.S. Marine Mammal Commission, contract MM7AC020. Available Natl. Tech. Inf. Serv., Springfield, Va., as PB 293380.

vestibular dysfunction." They also found no parasitic infiltration of the eighth cranial nerves or the vestibular cochlear nuclei.

We examined the reproductive organs from the six fresh carcasses. We judged the male to be sexually mature on the basis of body length (520 cm), total testis weight (8,200 g) and histological demonstration of spermatogenesis. We considered three of the females (body lengths 297, 338, 358 cm) sexually immature. Neither corpora lutea nor corpora albicantia were found in the ovaries (Harrison[13]) and ovary weight was low (13.3, 14.0, and 15.1 g, respectively) compared with the other two females. One female (475 cm) had three corpora albicantia in the left ovary and five to six corpora albicantia in the right ovary (Harrison see footnote 13). Ovary weight was 46.8 g. We also considered the 440 cm female from Redfish Pass to be sexually mature based on ovary weight (65 g) and the presence of three corpora albicantia in the left ovary and six in the right.

Few data are available on sexual maturity and reproduction in *P. crassidens*. Comrie and Adams (1938) examined four 425-450 cm female specimens of *P. crassidens* that were all sexually mature. Norman and Fraser (1948) and Purves and Pilleri (1978) stated that sexual maturity was reached in both sexes at 366-427 cm (12-14 ft) long. Using Norman and Fraser's length range, three females from the Tortugas stranding would be considered immature with the lower limit and nine with the upper limit, and three males would be considered immature with the upper limit.

Hematology

We took blood from vessels in the flukes, flippers, or dorsal fins. Samples for cell counts and hemoglobin determinations were collected in anticoagulant tubes. We collected sera from separate tubes after the blood had clotted, and stored it frozen until it was analyzed. Cell counts were done with a Coulter Model D-2 (Coulter Electronics, Hialeah, Fla.). Serum chemistry analyses were done with a Clinicard Model 368 (Harleco Div. American Hospital Supply Co., Gibbstown, N.J.). This is one of the few (if not the only) times when blood samples have been collected from an entire herd of stranded cetaceans. The data from the 30 Loggerhead Key animals are similar to hematologic values for other small cetaceans (Table 1; Ridgway et al. 1970; Ridgway 1972). Brown et al. (1966) gave some data on blood cell counts from the one false killer whale held at Marineland of the Pacific for 7 yr. Those values are roughly similar to those presented here, but red cell counts were higher ($4.5\text{-}5.2 \times 10^6/mm^3$). The blood values for our four female false killer whales (Table 1) vary somewhat from the Loggerhead Key group and undoubtedly reflect their deteriorating condition. Notable are leucocytosis with an eosinophilia in both groups (Table 1). Serum calcium levels were elevated when compared with other odontocetes. Lactic acid dehydrogenase levels were slightly elevated. All of the above conditions can be indicative of heat stress, parasitism, pneumonia, etc. in other odontocetes, and we assume that *P. crassidens* responds similarly. Alkaline phosphatase levels were low, indicating depletion of reserves. This depletion generally signals impending death in other odontocetes. Blood urea nitrogen and glucose levels were higher in the captives than in the Loggerhead Key animals and could reflect the fact that captives were feeding while the other group had probably not fed for several days. White blood cell counts and lactic acid dehydrogenase levels were the only parameters in which males and females differed significantly (t-test, 0.01 level).

Behavior in Captivity

The four live false killer whales transported to Sea World appeared to adapt to captivity with relative ease. When first put into their pool, they began to swim rapidly around the pool as a group, swimming in a clockwise direction with the largest animal (475 cm), apparently leading the group. They often took food from the hand and were not easily disturbed by routine handling for physical examinations. Within 24 h after their arrival, the largest and the smallest whales were separated from the other two and placed in an adjacent pool. The overall swimming patterns of all the animals remained the same after the separation. However, their swimming pace slowed considerably. The general behavior and apparent rapid adaptation to captivity was quite similar to that observed in a captive false killer whale (animal collected at sea) held at Marineland of the Pacific (Brown et al. 1966).

All of the animals began feeding on mackerel and herring immediately upon arrival. The 338

[13]Richard J. Harrison, Anatomy School, Cambridge University, Cambridge, Engl., pers. commun. 1976.

TABLE 1.—Blood chemistry analyses from two groups of the false killer whale, *Pseudorca crassidens*, stranded in Florida compared with data for the bottlenose dolphin, *Tursiops truncatus*, and the Pacific whitesided dolphin, *Lagenorhynchus obliquidens*.

Parameter	*P. crassidens*[1]			*P. crassidens*[2]			*T. truncatus*[3]		*L. obliquidens*	
	[4]*N*	$\bar{x}$	SD	*N*	$\bar{x}$	SD	*N*	$\bar{x}$	*N*	$\bar{x}$
Hemoglobin (g/100 ml)	26	15.95	0.84	23	14.27**	1.29	296	14.73*	67	18.61*
Hematocrit (%)	26	46.04	2.05	23	41.26**	3.22	345	44.04*	79	51.67*
Red cell count (10^6/mm^3)	26	4.01	0.27	23	3.80**	0.29	291	4.05*	64	5.56*
Mean corpuscular hemoglobin (pg)	26	39.85	2.04	23	37.53**	2.28	—	[5]36.37	—	33.4*
Mean corpuscular volume μ^3	26	115.02	4.61	23	108.70**	6.47	—	[5]108.74	—	92.93
Mean corpuscular hemoglobin conc. (g/dl)	26	34.64	0.95	23	34.56	1.53	—	[5]33.45	—	[5]36.02
White cell count (10^3/mm^3):										
Females	15	7,324*	1,765	23	8,842	3,434	167	9,780*	31	6,668*
Males	11	5,922*	1,203	—	—	—	154	10,675*	41	7,922*
Differential white cell count:										
Bands (immatures) (%)	26	1.31	2.02	23	1.83	2.21	318	1	72	1
Neutrophils (%)	26	73.31	12.43	23	71.83	10.82	318	61	72	42
Lymphocytes (%)	26	13.50	6.59	23	16.96	7.30	318	21	72	29
Eosinophils (%)	26	13.38	9.65	23	9.17	7.65	318	14*	72	22
Monocytes (%)	26	0.58	0.86	23	0.43	0.73	318	3	72	5
Basophils(%)	26	0	0	23	0	0	—	—	—	—
Blood urea nitrogen (mg/100 ml)	29	24.40	4.91	20	46.40**	14.82	232	51*	62	37
Calcium (mg/100 ml)	29	10.67	2.01	17	8.67**	0.56	166	10	29	10
Creatinine phosphokinase (IU/liter)	28	22.93	16.09	13	86.77**	134.82	—	—	—	—
Total cholesterol (mg/100 ml)	29	218.17	47.30	20	305.00**	87.38	301	221	92	154
Lactic acid dehydrogenase (IU/liter)										
Females	17	566.24	80.65	17	364.65**	76.52	100	113	11	179
Males	12	508.83	56.83	—	—	—	80	130	18	244
Alkaline phosphatase (IU/liter)	29	98.72	56.51	20	149.15**	113.80	71	241*	6	256*
Serum glutamic oxaloacetic transaminase (IU/liter)	29	217.52	88.46	20	382.15**	166.82	172	98*	34	110*
Serum glutamic pyruvic transaminase (IU/liter)	29	43.03	63.58	20	31.89**	28.43	88	19	14	45
Glucose (mg/100 ml)	29	80.76	28.76	20	167.10**	52.34	231	129	52	117
Total protein (g/100 ml)	29	7.60	0.56	20	7.32	0.85	133	8.0	10	9.0
Albumin (g/100 ml)	29	3.55	0.34	20	3.71	0.40	109	3.4	10	3.9
Globulin (g/100 ml)	29	3.91	0.73	20	3.55	0.75	—	—	—	—

[1]Animals from Loggerhead Key; each animal sampled once
[2]The four females held at Sea World; each animal sampled several times.
[3]Data from Ridgway et al. (1970).
[4]Number of determinations made
[5]Values calculated using mean values for hematocrit, hemoglobin and red cell count.
*Significant difference between males and females, *t*-test, 0.01 level.

cm female consumed an average (±SD) of 20±7.6 kg of mackerel and herring/day, in a ratio of 1.5:1, from 25 July through 9 August. Food consumption decreased significantly on 10 August and the animal died on 13 August. Similarly, the 297 cm female consumed 15.3±4.0 kg of mackerel and herring (2.2:1) between 24 July and 3 August. Food consumption dropped to 1.8 kg on 4 August, rose to 18.6 kg on 8 August when smelt was added to the diet, and then decreased to 5.4 kg on 13 August. Overall food consumption between 24 July and 13 August was 11.7±5.7 kg/day. The animal died on 14 August. The 358 cm female consumed 15.1±8.5 kg of mackerel and herring/day (1.2:1) between 24 July and 7 August. Food consumption decreased on 4 August and remained stable through 7 August ($\bar{x}$ = 9.0±2.5 kg/day). Consumption between 24 July and 3 August was 17.1±8.9 kg/day. Smelt was introduced on 8 August in place of mackerel and total consumption was 22.7 kg. Squid was also added on 9 August. The animal died on 10 August. The 475 cm female had an erratic food consumption (mackerel and herring, 19.4±16.2 kg/day) between 24 July and 29 July when it died. The individual blood chemistry analyses for these four animals reflected their deteriorating condition (Odell et al. see footnote 8) and their combined values were significantly different from the Loggerhead Key animals (Table 1).

Relationships Among Strandings

It is clear, based on photographs, that some of the false killer whales that left Pine Island Sound were the same individuals that stranded on Loggerhead Key. Low altitude (helicopter) aerial photographs were taken of the animals leaving Captiva Pass (Larson see footnote 3). Comparison of these photographs with photographs of dorsal fins of the Tortugas animals provided positive identification of several individuals. Dorsal fin shapes have been used to identify specific individual dolphins over periods of several months

(Würsig and Würsig 1977). Assuming that the animals left Captiva Pass at about 1200 h on July 22, and that they travelled in a straight line, they had to travel about 80 km/day to reach Loggerhead Key at 1300 h on 25 July. When these animals were escorted away from Loggerhead Key on 27 July, they apparently headed northeast (Schimpff[14]). The dead animals we found on Cape Sable were too decomposed to tell if they were the Captiva-Tortugas animals. Three large black whales were seen by a National Park Service pilot several kilometers east of the Dry Tortugas when the other animals were stranded. These may be the first three animals found floating off Cape Sable on 2 August by Park Service personnel, but the evidence is only circumstantial.

The sequence of strandings described herein roughly parallels a series of pilot whale, *Globicephala macrorhynchus*, strandings that occurred in the same vicinity on 19-20 August 1971 (Fehring and Wells 1976). Forty-four pilot whales stranded on Manasota Key and on Gasparilla Island a few kilometers to the south (Figure 1). On 25 August 1971, 12 or 13 pilot whales were found stranded on the Marquesas Keys east of Key West (Figure 1). At least one of these was positively identified to be from the previous stranding.

Fehring and Wells (1976) reported that the pilot whales observed stranding on Gasparilla Island made "a deliberate shoreward movement" as opposed to "disoriented panic." Eugene Shinn (see footnote 5) unknowingly photographed the false killer whales minutes before they beached on Loggerhead Key while taking aerial photographs of the reef formations. The photographs show two close-knit pods of whales heading towards the beach. Fehring and Wells also reported that the behavior of the stranded animals changed after the two largest pilot whales were towed offshore and held there with ropes around their caudal peduncles. The remainder of the animals then showed less tendency to return to shore when pushed off. Several of the larger Loggerhead Key whales were forced offshore (headfirst, without ropes around their tails) in hope that the others would follow. The animals herded offshore returned to the beach when released. The operation was only successful when all of the animals were forced offshore simultaneously and herded to deeper water, using swimmers and two boats. While on the Loggerhead Key beach, the whales were docile, as Fehring and Wells (1976) reported for the pilot whales. Coast Guard personnel who followed the animals offshore reported that the herd split into two groups (one of 17-18 and one of 10 or 11 animals) (Schimpff see footnote 14).

[14]Robert Schimpff, Department of Pathology, College of Medicine, University of Florida, Gainesville, FL 32610, pers. commun. 1977.

Conclusions

From the veterinary medical standpoint, we would doubt the ability of those animals that were necropsied to function normally with the heavy parasite load in the pterygoid sinus complexes. The benefits of forcing live stranded animals back out to sea must be carefully weighed against the benefits of bringing them into captivity, where they can be observed closely and thoroughly necropsied should death occur. If stranded whales are returned to sea, they should be given permanent, individual identification marks (e.g., freeze brands) and, ideally, outfitted for radio tracking.

Acknowledgments

The data presented in this paper could not have been collected without the generous assistance of many organizations and individuals, including the Florida Marine Patrol, U.S. Coast Guard, U.S. National Park Service, National Marine Fisheries Service, Wometco Miami Seaquarium, Gary Davis, Gary Hendrix, Deke Buesse, Ralph Miele, John Reynolds, and others. Material from the four captive animals at Sea World was examined as follows: ovaries - Richard J. Harrison; parasites - Robin M. Overstreet; histopathology - Armed Forces Institute of Pathology. Gordon Hubbell kindly provided the information on the 1972 stranding. Donald Forrester, Robert Schimpff, and Nicholas Hall commented on an early draft of this paper. William F. Perrin, James G. Mead, and Edward D. Houde provided useful criticisms on a later draft.

Literature Cited

ASH, C. E.
1952. The body weights of whales. [In Engl. and Norw.] Nor. Hvalfangst-Tidende 41:364-374.
1953. Weights of Antarctic humpback whales. Nor. Hvalfangst-Tidende 42:387-391.

BEAUCHAMP, J. J., AND J. S. OLSON.
1973. Corrections for bias in regression estimates after logarithmic transformation. Ecology 54:1603-1607.

BROWN, D. H., D. K. CALDWELL, AND M. C. CALDWELL.
1966. Observations on the behavior of wild and captive false killer whales, with notes on associated behavior of other genera of captive delphinids. Bull. Los. Ang. Cty. Mus. Nat. Hist. Sci. 95, 32 p.
BRYDEN, M. M.
1972. Growth and development of marine mammals. *In* R. J. Harrison (editor), Functional anatomy of marine mammals, Vol. I, p. 1-79. Acad. Press, N.Y.
CALDWELL, D. K., M. C. CALDWELL, AND C. M. WALKER, JR.
1970. Mass and individual strandings of false killer whales, *Pseudorca crassidens*, in Florida. J. Mammal. 51:634-636.
COMRIE, L. C., AND A. B. ADAMS.
1938. The female reproductive system and corpora lutea of the false killer whale, *Pseudorca crassidens* Owen. Trans. R. Soc. Edinb. 59(2):521-531.
DUDOK VAN HEEL, W. H.
1962. Sound and Cetacea. Neth. J. Sea. Res. 1:407-507.
FEHRING, W. K., AND R. S. WELLS.
1976. A series of strandings by a single herd of pilot whales on the west coast of Florida. J. Mammal. 57:191-194.
FUJINO, K.
1955. On the body weight of the sei whales located in the adjacent waters of Japan (II). Whales Res. Inst. Sci. Rep. 10:133-139.
MARELLI, C. A.
1953. Documentos iconigraficos sobre cetaceos de las costa Argentinas. Ann. Nahuel Huapi 3:133-143.
MITCHELL, E.
1975a. Porpoise, dolphin, and small whale fisheries of the world; status and problems. Int. Union Conserv. Nat. Nat. Resour., Monogr. 3, 129 p.
MITCHELL, E. D. (editor).
1975b. Review of biology and fisheries for smaller cetaceans. Report of the meeting on smaller cetaceans, Montreal April 1-11, 1974, subcommittee on small cetaceans, scientific committee, International Whaling Commission. J. Fish. Res. Board Can. 32:889-983.
NORMAN, J. R., AND F. C. FRASER.
1948. Giant fishes, whales, and dolphins. Putnam, Lond., 376 p.
OMURA, H.
1950. On the body weight of sperm and sei whales located in the adjacent waters of Japan. Whales Res. Inst. Sci. Rep. 4:1-13.
PORTER, J. W.
1977. *Pseudorca* stranding. Oceans 10(4):8-16.
PURVES, P. E., AND G. PILLERI.
1978. The functional anatomy and general biology of *Pseudorca crassidens* (Owen) with a review of hydrodynamics and acoustics in Cetacea. Invest. Cetacea 9:67-227.
REIGER, G.
1975. Dolphin sacred, porpoise profane. Audubon 77(1):2-29.
RIDGWAY, S. H.
1972. Homeostasis in the aquatic environment. *In* S. H. Ridgway (editor), Mammals of the sea: biology and medicine, p. 590-747. Charles C. Thomas, Springfield, Ill.
RIDGWAY, S. H., J. G. SIMPSON, G. S. PATTON, AND W. G. GILMARTIN.
1970. Hematologic findings in certain small cetaceans. J. Am. Vet. Med. Assoc. 157:566-575.
SERGEANT, D. E., AND P. F. BRODIE.
1969. Body size in white whales *Delphinapterus leucas*. J. Fish. Res. Board Can. 26:2561-2580.
TOMILIN, A. G.
1957. Mammals of the U.S.S.R. and adjacent countries. Vol. 9. Cetacea. [In Russ.] Izd. Akad. Nauk. SSSR, Mosk., 756 p. (Translated by Isr. Program Sci. Transl., Jerusalem, 1967, 717 p.)
WÜRSIG, B., AND M. WÜRSIG.
1977. The photographic determination of group size, composition, and stability of coastal porpoises (*Tursiops truncatus*). Science (Wash., D.C.) 198:755-756.

DANIEL K. ODELL

Division of Biology and Living Resources
Rosenstiel School of Marine and Atmospheric Science
University of Miami
4600 Rickenbacker Causeway, Miami, FL 33149

EDWARD D. ASPER
JOE BAUCOM

Sea World, Inc.
7007 Sea World Drive
Orlando, FL 32809

LANNY H. CORNELL

Sea World, Inc.
1720 South Shores Road
San Diego, CA 92109

OCCURRENCE OF THE FINETOOTH SHARK, *CARCHARHINUS ISODON*, OFF DAUPHIN ISLAND, ALABAMA[1]

Carcharhinus isodon (Valenciennes) is an infrequently encountered species with a poorly known life history. The literature on this species covering the western North Atlantic contains much information on juveniles, but very little on adults. All lengths discussed herein are total lengths.

Radcliffe (1916) reported a single specimen 50.8 cm in the Bureau of Fisheries collection at Beaufort, N.C. Burton's (1940) record of an immature male, 74.4 cm, was the first from South Carolina waters. Specimens examined by Bigelow and Schroeder (1948:304-308) ranged from 46 to 56.7 cm. Springer (1950) examined 20 adult females 147-155 cm collected in December off Salerno, Fla. Thirteen had from one to six embryos 43-48 cm; the remaining seven had enlarged flaccid uteri and medium-sized ovarian

[1]Contribution No. 028, Dauphin Island Sea Lab.

eggs. He suggested a winter pupping period. Clark and von Schmidt (1965) recorded only a single female (76 cm) in 9 yr of shark research off Sarasota, Fla. Dahlberg and Heard (1969) reported the capture of 30 individuals from July through September 1968 off Georgia. Of these, 29 were between 52 and 94 cm. The other specimen (144 cm) was probably the only mature individual, although there was no mention of sex or reproductive development. Hoese and Moore (1977, appendix 5) listed *C. isodon* as a spring through fall spawner based on collections of juveniles at Port Aransas, Texas. Compagno (1978), in his review of the species, assigned this species to the genus *Carcharhinus*.

During longlining operations in the northern Gulf of Mexico in summer 1978, a gravid female and two males were collected off Dauphin Island, Ala. On 2 July 1979 one male and one female were collected in the mouth of Mobile Bay. With so few reports of mature *C. isodon*, these captures will serve to better define the reproductive life history of this species.

On 5 June 1978 the gravid female (139 cm) was collected by longline in water about 5 m deep, approximately 1 km southwest of Sand Island, a small barrier island approximately 5 km south of the east end of Dauphin Island. The shark carried four embryos ranging from 49 to 51 cm. These appeared to be near-term pups. There were two pups in each uterus, each positioned with the head toward the anterior end of the uterus. Each pup was enveloped by a membrane which was filled anteriorly with a translucent yellow fluid. Each had a highly vascularized placenta attached to the posterior portion of the uterus, and the connecting umbilical cords measured 20.6-30.0 cm. Where an umbilical cord attached to a placenta there were three saclike extensions containing a small amount of clear fluid. In earlier embryonic stages of other species of carcharhinid sharks these sacs contain the remaining unconsumed portion of the yolk (Gilbert and Schlernitzauer 1966). The left uterus contained two males; the right uterus one male and one female. The pups and jaws of the female were deposited in the

TABLE 1.—Measurements (centimeters; methods after Bass et al. 1973) of the gravid female *Carcharhinus isodon* and the four pups.

Item	Gravid female	Pup no. 1 male	Pup no. 2 male	Pup no. 3 male	Pup no.4 female
Total length	139	49	51	50.5	50.5
Fork length	118	38.5	40.5	40	40.5
Standard length	106	35	37	36	36.5
Snout to:					
Dorsal 1	46	15.7	16.5	16.5	16.5
Dorsal 2	90	30.2	31.5	31	32.5
Pectoral fin	31.5	11	12.2	11.9	12.2
Pelvic fin	74	22.8	25.4	23.8	24.2
Anal fin	88	28.9	31.9	31.3	30.4
Mouth	9	3.9	3.9	3.8	3.8
Mouth breadth	13	4.1	4.4	4.2	4.1
Between nostrils	7	2.7	2.7	2.7	2.8
Eye diameter	1.8	.8	.8	.8	.7
Gill lengths:					
No. 1	8	2.5	2.3	2.2	2.3
No. 2	8.6	2.6	2.5	2.4	2.5
No. 3	9	2.7	2.7	2.6	2.6
No. 4	8.5	2.5	2.4	2.3	2.4
No. 5	7.5	2.1	1.8	1.8	1.8
Dorsal 1 height	14.7	3.9	3.8	3.5	3.8
Dorsal 1 base	14	4.3	4.6	4.6	5.1
Dorsal 1 free margin	5.5	2.0	2.2	1.8	2.0
Dorsal 2 height	4.0	1.2	1.4	1.4	1.1
Dorsal 2 base	6.5	1.9	2.2	2.2	2.1
Dorsal 2 free margin	5.5	2.0	2.2	1.9	1.9
Anal height	4.3	1.4	1.5	1.5	1.3
Anal base	7.4	2.2	2.4	2.4	2.1
Anal free margin	4.8	1.9	1.9	1.8	1.8
Pectoral height	22	6.0	6.9	6.3	6.5
Pectoral base	8	2.5	2.6	2.5	2.5
Pectoral free margin	6.5	2.2	2.4	2.4	2.4
Pelvic anterior margin	6.5	2.4	2.6	2.7	2.8
Pelvic distal margin	8.8	2.8	2.9	2.7	2.8
Uppper caudal length	39	13.8	14.9	14.7	14.1
Lower caudal length	17.5	5.1	5.5	5.1	5.4
Interspace base dorsal 1 to origin dorsal 2	33	10.1	10.2	9.9	10.3
Interspace base dorsal 2 to caudal pit	10.5	3.8	3.9	3.4	3.4
Origin of pectoral to origin of pelvic	42	11.8	13.2	11.9	12.0
Origin of pelvic to origin of anal	16	6.1	6.5	7.5	6.2
Weight (g)	-	704	810	737	758

University of South Alabama Ichthyological Collection (USAIC 6278). Measurements and weights are found in Table 1.

Since most records of *C. isodon* are of juveniles, there is little information on the reproductive biology of the species. Based on the cited literature and these data, pups appear to be 45-55 cm at birth. However, seasonality is uncertain as the records of Springer (1950) are not in accord with those of either Hoese and Moore (1977) or this report.

Length at maturity can be closely estimated. One male (112 cm) collected 13 July 1978 was immature—based on incomplete calcification of the claspers and incompletely developed siphon sacs, each sac being 7.5 cm long and 1.0 cm wide. The other two males (120 and 127 cm) collected 2 July 1979 and 28 June 1978 had well-calcified claspers and fully developed siphon sacs. The only literature on mature males (Springer 1950) listed lengths of 140-152 cm. Males apparently mature between 115 and 120 cm. Maturity in females must be reached at a larger size. The female collected in July 1979 was 127 cm, yet was immature with only small undeveloped ovarian eggs. The gravid female reported here was 139 cm, and those reported by Springer (1950) were 147-155 cm.

Carcharhinus isodon was only collected when similarly sized specimens of blacktip shark, *C. limbatus*, were caught: 3 *C. limbatus* (126-166 cm) with the gravid female, 12 *C. limbatus* (102-117 cm) with the 112 cm male, 2 *C. limbatus* (111 and 124 cm) with the 127 cm male, and 12 *C. limbatus* (100-130 cm) with the two specimens caught in 1979. If *C. isodon* is an uncommon straggler into the northern Gulf of Mexico it may be schooling with other sharks of like size. Sharks that school have been noted to do so by sex or size (Ford 1921).

Literature Cited

BASS, A. J., J. D. D'AUBREY, AND N. KISTNASAMY.
1973. Sharks of the east coast of Southern Africa. I. The genus *Carcharhinus* (Carcharhinidae). Oceanogr. Res. Inst. (Durban), Invest. Rep. 33, 168 p.

BIGELOW, H. B., AND W. C. SCHROEDER.
1948. Sharks. *In* Fishes of the western North Atlantic. Part one, p. 59-546. Mem. Sears Found. Mar. Res., Yale Univ. 1.

BURTON, E. M.
1940. *Aprionodon isodon* from South Carolina. Copeia 1940:140.

CLARK, E., AND K. VON SCHMIDT.
1965. Sharks of the central Gulf Coast of Florida. Bull. Mar. Sci. 15:13-83.

COMPAGNO, L. J. V.
1978. Sharks. *In* W. Fischer (editor), FAO species identification sheets for fishery purposes: western central Atlantic. Vol. 5, unpaginated.

DAHLBERG, M. C., AND R. W. HEARD, III.
1969. Observations on elasmobranchs from Georgia. Q. J. Fla. Acad. Sci. 32:21-25.

FORD, E.
1921. A contribution to our knowledge of the life-histories of the dogfishes landed at Plymouth. J. Mar. Biol. Assoc. U.K. 12:468-505.

GILBERT, P. W., AND D. A. SCHLERNITZAUER.
1966. The placenta and gravid uterus of *Carcharhinus falciformis*. Copeia 1966:451-457.

HOESE, H. D., AND R. H. MOORE.
1977. Fishes of the Gulf of Mexico, Texas, Louisiana, and adjacent waters. Tex. A&M Univ. Press, College Station, 327 p.

RADCLIFFE, L.
1916. The sharks and rays of Beaufort, North Carolina. Bull. U.S. Bur. Fish. 34:239-284.

SPRINGER, S.
1950. A revision of North American sharks allied to the genus *Carcharhinus*. Am. Mus. Novit. 1451, 13 p.

STEVEN BRANSTETTER
ROBERT L. SHIPP

University of South Alabama
Dauphin Island Sea Lab
P.O. Box 386
Dauphin Island, AL 36528

SHEDDING RATES OF PLASTIC AND METAL DART TAGS FROM ATLANTIC BLUEFIN TUNA, *THUNNUS THYNNUS*[1]

In 1971, the International Commission for the Conservation of Atlantic Tunas (ICCAT) recommended that a double-tagging experiment be conducted on Atlantic bluefin tuna, *Thunnus thynnus*, to determine whether plastic or metal dart tags were more efficient and to estimate immediate and instantaneous tag shedding rates. A knowledge of shedding rates is necessary so that appropriate adjustments can be made when estimating mortality rates from tag return data. This study was begun in 1971 by the National Marine Fisheries Service (NMFS), the Woods Hole Oceanographic Institution (WHOI), and the Fisheries Research Board of Canada (FRBC). The

[1]Southeast Fisheries Center Contribution Number 80-14M.

results obtained through 1972, for 580 double-tagged bluefin tuna released during 1971 off the east coast of the United States, were reported by Lenarz et al. (1973). Their results were partially based on tags supplied by the FRBC, some of which had longer streamers than the tags supplied by WHOI. For our present analysis, we used only data from the WHOI tags.

In this paper we present the overall findings obtained through 1978 for 3,121 double-tagged bluefin tuna. These fish were released primarily from U.S. purse seine vessels fishing off the east coast of the United States from Virginia to Massachusetts from 1971 through 1977.

Methods

The U.S. double-tagging program for Atlantic bluefin tuna was conducted jointly by the NMFS and WHOI. Tags and tagging procedures were those described by the Food and Agriculture Organization (1972). All fish were tagged and released from U.S. purse seine vessels (98% of all releases) and from a few sport fishing vessels. Tagging occurred throughout the purse seine fishing season during 1971, 1973, and 1974, and at the end of the season during 1972, 1975, 1976, and 1977. The double-tagging operation was conducted entirely by John Mason during each year except 1974, when two assistants aided in the double tagging. Precise release dates were available for all of the fish. In a few instances only the month and year were known for the recapture data. In these cases, the 15th of the month was arbitrarily selected to represent the recapture date. The vast majority of returns fall into an annual cycle during which the recapture periods are approximately 2-3 summer months. The interval midpoints of the time intervals can be considered to be on a yearly cycle. Therefore, we grouped returns into "first year returns," "second year returns," etc., and calculated average days out from the individual days out for each return. Tag shedding rates were estimated using the notation and methodology of Bayliff and Mobrand (1972) for yellowfin tuna, which Lenarz et al. (1973) used for bluefin tuna and Laurs et al. (1976) used for North Pacific albacore. Chapman et al. (1965) developed the original model with the assumption of only one type of shedding which occurs at a constant instantaneous rate. Bayliff and Mobrand (1972) assumed that there are two types, Type I which occurs immediately after the fish are released and Type II, the type described by Chapman et al. (1965).

Bayliff and Mobrand's modifications[2] of the Chapman et al. (1965) approximate equations for tag returns of double-tagged fish are:

$$n_{ddk} = F\tau N_D\ \pi\rho^2 \exp-(F+X+2L)t_k \qquad (1)$$

$$n_{dsk} = 2F\tau N_D\ \pi\rho(1-\rho\exp(-Lt_k))\ \exp(-(F+X+L)t_k) \qquad (2)$$

where n_{ddk} = number of returns of double-tagged fish retaining both tags caught during the recapture period t_k,

n_{dsk} = number of returns of double-tagged fish retaining only one tag caught during the period t_k,

F = instantaneous rate of fishing mortality,

N_D = number of double-tagged fish released,

π = proportion of tagged fish which remain alive after the Type-I mortality (immediate) has taken place,

ρ = proportion of the tags which are retained after Type-I shedding (immediate) has taken place,

X = instantaneous rate of mortality due to natural causes, Type-II tagging mortality (long term), and emigration from the fishing grounds,

L = instantaneous rate of tag shedding (Type II), and

t_k = time at the middle of the kth recapture period of length τ ($k = 1, 2, 3$).

From Equations (1) and (2) it follows that

$$\frac{n_{dsk}}{n_{ddk}} = \frac{2(1-\rho\exp(-Lt_k))\exp(Lt_k)}{\rho}$$

and therefore

$$\frac{n_{dsk}}{2n_{ddk}} = \frac{\exp(Lt_k)-\rho}{\rho} = \frac{\exp(Lt_k)}{\rho} - \frac{2n_{ddk}}{2n_{ddk}}.$$

Rearranging terms yields

[2] As pointed out by Laurs et al. (1976), there was typographical error in both Bayliff and Mobrand (1972) and Lenarz et al. (1973) in Equation (2).

$$\frac{2n_{ddk}}{n_{dsk} + 2n_{ddk}} = \rho\exp(-Lt_k)$$

and hence $$\ln\frac{2n_{ddk}}{n_{dsk} + 2n_{ddk}} = \ln\rho - Lt_k = Y_k$$

where Y_k is an estimate of the natural logarithm of the proportion of tags retained up to time t_k. Given n_{ddk}, n_{dsk}, and t_k, then L and ρ can be estimated using linear regression. We first estimated these parameters using the usual least-squares linear regression which assumes homoscedasticity. We also believed that it would be appropriate to consider that variability may increase as a function of time as the number of recoveries decreases. To accomplish this, a weighting factor was introduced and a weighted least-squares linear regression model was fitted to calculate values of $\ln\hat{\rho}$ and $\hat{L}$, as was done by Bayliff and Mobrand (1972). The weights for each time interval k ($k = 1, 2, 3$) were equated to the ratio of the number of returns of double-tagged fish during interval k to the total number of returns of double-tagged fish during all k-periods. This can be simply expressed as:

$$\omega_k = \frac{n_{ddk} + n_{dsk}}{\sum_{i=1}^{3}(n_{ddi} + n_{dsi})}.$$

While we consider this a reasonable first approximation of the correct weight, further investigations of the statistical properties of Y_k to formally determine the correct weighting procedure are desirable. Estimates of $\ln\rho$ and L were then made using weighted linear regression.

Results and Discussion

The double-tag releases during 1971 through 1977 and returns in 1971 through 1978 are shown by tag type (Table 1). A sufficient number of tag returns existed to allow examination of three separate recapture periods. Only a few returns existed from beyond the third recapture period. There were approximately equal numbers of each tag type released each year. Table 1 constitutes the basic data used throughout this study. Using the basic data, we estimated values of immediate (Type I) and instantaneous (Type II) shedding rates for each tag type. Further, we tested several hypotheses including: 1) equality of return rates for same year recaptures; 2) equality of return rates by estimated age; and 3) differences in returns and nonreturns over 2 or 3 yr time periods for various time intervals.

Using the double-tagging release data for all years combined (1971-77) the return rate for plastic tags was 5.1% the first year, 8.6% the second year, and 1.6% the third year. The return rate for metal dart tags was 5.5% the first year, 9.1% the second year, and 2.9% the third year. Therefore, for both types of tags the return rates increased the second year and decreased the third year. This should be expected since tagging occurred at the end of the purse seine season for several of the release years studied. Chi-square tests (not cor-

TABLE 1.—Tag releases and returns from northwestern Atlantic bluefin tuna double-tag study. For each of $k = 1, 2$, or 3 recapture periods the number of returns of double-tagged fish retaining both tags is n_{ddk} and those retaining only one tags is n_{dsk}. The average number of days-at-large for each period is t_k.

Tag type	Double-tagged releases		First-year returns			Second-year returns			Third-year returns		
	Year	Number	n_{dd1}	n_{ds1}	t_1 (days)	n_{dd2}	n_{ds2}	t_2 (days)	n_{dd3}	n_{ds3}	t_3 (days)
Plastic dart (D-tag)	1971	150	4	0	7.25	20	9	349.07	3	1	724.00
	1972	75	6	0	12.83	17	4	340.52	1	1	726.50
	1973	134	18	2	18.45	6	4	354.20	0	1	708.00
	1974	629	25	4	12.07	18	12	352.17	4	7	727.82
	1975	50	0	1	40.00	1	1	384.50	0	0	0
	1976	267	12	2	16.36	2	2	341.00	1	2	707.33
	1977	223	3	1	47.50	25	4	361.83	—	—	—
	Total	1,528	68	10	16.46	89	36	352.06	9	12	723.10
Metal dart (H-tag)	1971	162	4	1	18.60	10	9	358.63	2	3	724.80
	1972	77	0	1	11.00	9	11	343.55	0	1	740.00
	1973	131	12	5	16.88	1	3	373.25	0	2	720.00
	1974	666	28	2	10.97	40	13	358.57	15	11	703.19
	1975	58	1	0	43.00	4	5	339.11	2	0	687.50
	1976	271	23	3	23.08	6	0	311.00	0	4	759.25
	1977	228	8	0	36.00	24	2	365.19	—	—	—
	Total	1,593	76	12	18.76	94	43	354.71	19	21	712.48
	Grand total	3,121	144	22	17.68	183	79	353.44	28	33	716.13

rected for continuity) showed that there were no significant differences at the 0.01 level, with 1 degree of freedom, in return and nonreturn rates between tag types for fish at liberty for 1, 2, or 3 yr (Table 2). However, returns were significantly better at the 0.05 level for metal tags in the third year. Further, there was no significant difference at the 0.01 level in the first-year return and nonreturn rates between the two types of dart tag, whether comparing each year individually or comparing all years combined (Table 3).

We also tested for differences in return and nonreturn rates between age-groups. Fish were aged from unpublished length-age tables (Rivas[3]). Chi-square values for fish tagged at ages 1, 2, 3, and 4+, were not significant at the 0.01 level (Table 4). The results of the chi-square test indicated that tag types and ages could be combined.

Unweighted and weighted linear regression models were used to estimate immediate tag shedding rate ($1 - \rho$) and instantaneous shedding rate (L) (Table 5). The unweighted model for both tags combined yielded an estimate of immediate tag shedding ($1 - \rho$) to be 0.040 (0.042 for the weighted model). The overall estimate of the instantaneous rate of tag shedding (L) on an annual basis using the model was 0.205 (0.186 for the weighted model). (The annual rate analog for L from the unweighted model is 0.19.) Therefore, the results from each model were similar. We chose to use the unweighted results, which give a slightly higher $\hat{L}$ value. While results of the chi-square test indicated that tag types could be combined, estimates were also made for each tag type separately to

[3]L. R. Rivas, Southeast Fisheries Center Miami Laboratory, Natl. Mar. Fish. Serv., NOAA, 75 Virginia Beach Drive, Miami, FL 33149.

TABLE 2.—Chi-square tests (df = 1) of equality of yearly return and nonreturn rates between double-tagged releases for 1971-77 combined, for $k = 1, 2$, or 3 yr at liberty, using plastic or metal dart tags on bluefin tuna in the northwestern Atlantic Ocean. The number of returns of double-tagged fish retaining both tags is n_{ddk} and those retaining only one tag is n_{dsk}.

	Plastic dart tags			Metal dart tags			
Return year (k)	Double-tagged releases	Total returns kth year ($n_{ddk} + n_{dsk}$)	Return rate	Double-tagged releases	Total returns kth year ($n_{ddk} + n_{dsk}$)	Return rate	Chi-square value
1	1,528	78	0.05105	1,593	88	0.05524	0.272
2	1,450	125	0.08621	1,505	137	0.09103	0.213
3	1,325	21	0.01585	1,368	40	0.02924	5.452*
		Average	0.05104			0.05850	

*$P \leq 0.05$.

TABLE 3.—Chi-square tests (df = 1) of equality of return and nonreturn rates between double-tagged releases recaptured the same year using plastic or metal dart tags on bluefin tuna in the northwestern Atlantic Ocean. The number of returns of double-tagged fish retaining both tags during the first year after release is n_{dd1}, and those retaining only one tag is n_{ds1}.

	Plastic dart tags			Metal dart tags			
Year	Double-tagged releases	Total returns same year ($n_{dd1} + n_{ds1}$)	Return rate	Double-tagged releases	Total returns same year ($n_{dd1} + n_{ds1}$)	Return rate	Chi-square value
1971	150	4	0.02667	162	5	0.03086	0.049
1972	75	6	0.08000	77	1	0.01299	3.884*
1973	134	20	0.14925	131	17	0.12977	0.209
1974	629	29	0.04610	666	30	0.04505	0.008
1975	50	1	0.02000	58	1	0.01724	0.011
1976	267	14	0.05243	271	26	0.09594	3.699
1977	223	4	0.01794	228	8	0.03509	1.280
Total	1,528	78	0.05105	1,593	88	0.05524	0.272

*$P \leq 0.05$.

TABLE 4.—Chi-square tests (df = 1) of equality of return and nonreturn rates by estimated age between double-tagged releases for all years 1971-77 combined, recaptured the same year, using plastic or metal dart tags on bluefin tuna in the northwestern Atlantic Ocean. The number of returns of double-tagged fish retaining both tags during the first year after release is n_{dd1} and those retaining only one tag is n_{ds1}.

	Plastic dart tags			Metal dart tags			
Estimated age at release	Double-tagged releases	Total returns same year ($n_{dd1} + n_{ds1}$)	Return rate	Double-tagged releases	Total returns same year ($n_{dd1} + n_{ds1}$)	Return rate	Chi-square value[1]
1	641	29	0.04524	647	31	0.04791	0.052
2	631	43	0.06815	656	43	0.06555	0.035
3	212	4	0.01887	226	12	0.05310	3.642
4+	44	2	0.04545	64	2	0.03125	0.148
	1,528	78		1,593	88		

[1]No values significant at $P = 0.05$.

TABLE 5.—Estimates of immediate $(1 - \hat{\rho})$ and annual instantaneous $(\hat{L})$ tag shedding rates for northwestern Atlantic bluefin tuna double-tagging study for all years combined (1971-77) based on a 3-yr return period using unweighted and weighted linear regression models. (The weights used in the weighted model were equated to the ratio of the number of returns of double-tagged fish during each return period to the total number of returns of double-tagged fish during all periods.)

Model and tag type	$1 - \hat{\rho}$	$\hat{L}$ (annual)
Linear regression:		
Plastic dart	0.027	0.22886
Metal dart	0.049	0.19201
Combined	0.040	0.20452
Weighted linear regression:		
Plastic dart	0.033	0.19200
Metal dart	0.049	0.18213
Combined	0.042	0.18596

indicate the magnitude of the variances of the estimates.

Our estimate of $(1 - \rho)$ is slightly greater than the overall estimate of 0.027 given for bluefin tuna from the northwest Atlantic by Lenarz et al. (1973). The difference is small relative to the precision of the estimates. Our estimate of $(1 - \rho)$ for northwest Atlantic bluefin tuna is less than the value of 0.10 reported for Pacific yellowfin tuna by Bayliff and Mobrand (1972) and the value of 0.12 reported for North Pacific albacore by Laurs et al. (1976).

Our estimate of L is less than the overall estimate of 0.31 reported by Lenarz et al. (1973) for bluefin tuna and the L estimate of 0.278 reported for yellowfin tuna by Bayliff and Mobrand (1972). Our L estimate is greater than the estimates of between 0.086 and 0.098 reported for albacore by Laurs et al. (1976).

As previously noted, there was no significant difference in return rates found for the two types of dart tags for 1971-77. However, from examination of the data presented in Table 1, there appeared to be changes occurring in the shedding rates of each type of tag and a difference between the 1971-73 and 1974-77 time intervals. Therefore, we calculated $(1 - \hat{\rho})$ and $\hat{L}$ for each time interval and conducted chi-square tests (df = 6) for differences in returns over three recapture periods ($k = 3$) between time intervals and between tag types (Table 6). We found significant differences between time intervals for each of the tag types and significant differences between tag types for each of the time intervals. The plastic dart tags became less efficient, i.e., $\hat{L}$ increased over the time intervals, and the metal dart tags improved, i.e., $\hat{L}$ decreased over the time intervals.

The model of Chapman et al. (1965), which was modified by Bayliff and Mobrand (1972), assumes constant L over recapture periods. We decided to examine values of L over the two pairs of recapture periods $k = (1, 2)$ and $k = (2, 3)$ to determine how well our data fit the model. Since only two recapture periods were used, L and $(1 - \rho)$ were estimated by solving two simultaneous equations.

TABLE 6.—Estimates of immediate $(1 - \hat{\rho})$ and annual instantaneous $(\hat{L})$ tag shedding rates for northwestern Atlantic bluefin tuna double-tagging study for time intervals 1971-73 and 1974-77 based on a $k = 3$-yr return period. (A contingency table, 7×2, was constructed containing the number of double and single returns for each of the three recapture periods plus the number of nonreturns for each tag type and each time interval.) Results of chi-square tests (df = 6) for differences in double and single tag returns and total nonreturns between time intervals and tag types over a 3-yr recapture period are given.

Tag type and time interval	$1 - \hat{\rho}$	$\hat{L}$ (annual)	Chi-square value
Plastic dart:			
1971-73	0.029	0.14838	64.286**
1974-77	0.023	0.28455	
Metal dart:			
1971-73	0.140	0.37163	33.489**
1974-77	0.007	0.17242	
1971-73:			
Plastic dart	0.029	0.14838	18.924**
Metal dart	0.140	0.37163	
1974-77:			
Plastic dart	0.023	0.28455	18.135**
Metal dart	0.007	0.17242	

**$P \leq 0.01$.

For the tag types and time intervals examined, there is an indication that $\hat{L}$ is not constant (Table 7). In fact, $\hat{L}$ increased in three out of four cases. The sequence of events could have happened due to chance alone, for if the changes in $\hat{L}$ came from a binomial distribution with $P = 0.5$, then the probability of $\hat{L}$ decreasing in three of the four cases or $\hat{L}$ increasing in three of the four cases is ≤ 0.25. However, $\hat{L}$ during the second time period is more than 60% $> \hat{L}$ in the first time period in three cases and only 16% $< \hat{L}$ in the first time period in the other case. While the data do not provide conclusive evidence that L is not constant, it would be dangerous to extrapolate beyond the time period used for analysis.

We previously noted that the 1974 releases were

TABLE 7.—Estimates of annual instantaneous $(\hat{L})$ tag shedding rates for northwestern Atlantic bluefin tuna double-tagging study for 1971-73 and 1974-77 based on return periods of $k = (1, 2)$ and $k = (2, 3)$.

Tag type and time interval	Return period k	$\hat{L}$ (annual)
Plastic 1971-73	1, 2	0.16017
	2, 3	0.13421
Plastic 1974-77	1, 2	0.09925
	2, 3	0.45207
Metal 1971-73	1, 2	0.27858
	2, 3	0.45271
Metal 1974-77	1, 2	0.09331
	2, 3	0.24632

unique in that three individuals conducted the tagging operation, whereas only one individual tagged and released the remainder of the fish from the other years. Therefore, we analyzed the data from the time intervals 1971-73 and 1975-77 separately from the 1974 data. For the following reasons we decided to examine only two recapture periods, $k = (1, 2)$: 1) 1977 has only two recapture periods possible (Table 1); 2) the number of single as well as double returns for $k = 3$ for both 1971-73 and 1975-77 constitutes very small sample sizes (Table 1); and 3) L appears to have been changing over $k = (1, 2)$ to $k = (2, 3)$ (Table 7).

Our analysis showed (Table 8) that there was a significant difference in return and nonreturn rates between time intervals for each type of dart tag. Also a significant difference in shedding rates was found between the plastic and metal type tags during the time interval 1971-73. A small sample size may account for the lack of a significant difference in shedding rates for each type of tag during the time interval of 1975-77. There also was no significant difference found in the shedding rates between each tag type during 1974. As previously mentioned, fish were released under different circumstances during 1974. During the 1971-73 time interval, plastic tags were found to be superior. We again found that the metal tag improved (Table 8), i.e., $\dot{L}$ decreased, between 1971-73 and 1975-77.

TABLE 8.—Estimates of immediate $(1 - \hat{\rho})$ and annual instantaneous $(\dot{L})$ tag shedding rates for northwestern Atlantic bluefin tuna double-tagging study for 1971-73, 1974, and 1975-77 based on a $k = 2$-yr return period. (A contingency table, 7×2, was constructed containing the number of double and single returns for each of the three recapture periods plus the number of nonreturns for each tag type and each time interval.) Results of chi-square tests (df = 4) for differences in double and single tag returns and total nonreturns between time intervals and tag types over a 2-yr recapture period are given. (Results for the period 1971-72 from Lenarz et al. (1973) are shown for comparison.)

Tag type and time interval	$1 - \hat{\rho}$	$\dot{L}$	Chi-square value
Plastic dart:			
1971-73	0.028	0.16017	39.460**
1975-77	0.118	<0.	
Metal dart:			
1971-73	0.169	0.27858	22.186**
1975-77	0.114	0.05860	
1971-73:			
Plastic dart	0.028	0.16017	17.323**
Metal dart	0.169	0.27858	
1974:			
Plastic dart	0.067	0.22615	8.318
Metal dart	0.031	0.12126	
1975-77:			
Plastic dart	0.118	<0.	6.636
Metal dart	0.114	0.05860	
1971-72:			
Plastic dart	0.000	0.21615	
Metal dart	0.099	0.26278	

**$P \leq 0.01$.

Also, $\dot{L}$-values for the plastic tag decreased, but results yielded a negative value for the 1975-77 time interval, which is theoretically impossible and is due to variability in the data.

From our analysis, we cannot conclusively show that one of the two types of dart tags is better for bluefin tuna tagging. Both tag types appeared to improve between 1971-73 and 1975-77. Plastic tags were significantly better than metal in the first period and nonsignificantly better in the second.

We have shown that tag shedding rates vary from 1 yr to another. There are some possible reasons for the observed variability. One reason may be changes in tag design or quality. To our knowledge there was no intentional effort made by the manufacturers to change the design of the metal or plastic dart tags used in this study. A different type of glue, however, was used during 1972 through 1977 for the plastic dart tags. Before using the plastic dart tags, we tested them by pulling on the barb. On several occasions, we discovered that the barbs were not adequately secured. We reglued these tags before using them. We also examined the metal dart tags prior to their use. In general, they appeared to be trouble free. Several orders of both types of tags were used during the course of this study. We were unable to correlate changes in the shedding rates with the specific batch of tags that were used. The shelf life of the plastic used in the tags may be another factor. In some instances we used tags which were manufactured several years before their actual use. Since there were no changes in the tagging method, this reason was discounted. Tagging occurred throughout the purse seine fishing season during 1971, 1973, and 1974, and at the end of the season during 1972, 1975, 1976, and 1977. We do not see why this would have more of an effect on one type of tag than on the other.

Summary and Conclusions

Return data for double-tagged northwestern Atlantic bluefin tuna were used to estimate the shedding rates of plastic and metal dart tags. No significant difference was found between the return rates of the plastic and metal tags when the data were tested for all years combined, but plastic tags appeared to have lower shedding rates than metal tags in most cases. We believe that the combining of the data of all years together (1971-77) probably yields a reasonable approximation to the

average shedding rate for each type of tag. Type-I shedding, which occurs immediately after release, was estimated to be 0.040 for plastic and metal dart tags combined. Type-II (instantaneous) shedding was estimated to be 0.205 for plastic and metal tags combined on an annual basis.

The shedding rates for each type of tag were found to vary over the time period studied, and deviations from the assumption of constant shedding throughout the life of the tagged fish were noted. Due to these differences, one should not be satisfied with the results of one double-tagging experiment. We recommend that double tagging be employed whenever possible, as long as shedding occurs and the rate of shedding is found to vary. Also, tagged fish, especially the ones which have been at liberty for a long time, are more likely to continue to carry at least one tag if they were originally double tagged. The ones that do not continue to carry at least one tag are of no value. Furthermore, relative to the errors inherent in a study of this type we do not feel that there is really any important difference in shedding rates between the plastic and metal dart tags.

Since shedding may increase with time from release, extrapolations based on the assumption of constant L should be made with caution. Also because the tag shedding rates that we found are considerable, efforts should be made to develop a more efficient type of tag with a lower rate of shedding.

Acknowledgments

We thank W. H. Bayliff of the Inter-American Tropical Tuna Commission and J. Wetherall of the Southwest Fisheries Center Honolulu Laboratory, NMFS, NOAA, for their helpful comments on the manuscript. We also thank all captains and crewmen of commercial and sport fishing vessels, WHOI personnel, George Bell, NMFS personnel, Andy Bertolino, and Dennis Lee, who participated in the bluefin tuna tagging program, and T. Chewning of the Southeast Fisheries Center for computer programming assistance.

Literature Cited

BAYLIFF, W. H., AND L. M. MOBRAND.
1972. Estimates of the rates of shedding of dart tags from yellowfin tuna. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm., Bull. 15:439-462.

CHAPMAN, D. G., B. D. FINK, AND E. B. BENNETT.
1965. A method for estimating the rate of shedding of tags from yellowfin tuna. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm., Bull. 10:333-352.

FOOD AND AGRICULTURE ORGANIZATION.
1972. Final report of the working party on tuna and billfish tagging in the Atlantic and adjacent seas. FAO Fish. Rep. 118, Suppl. 1, 37 p.

LAURS, R. M., W. H. LENARZ, AND R. N. NISHIMOTO
1976. Estimates of rates of tag shedding by North Pacific albacore, *Thunnus alalunga*. Fish. Bull., U.S. 74:675-678.

LENARZ, W. H., F. J. MATHER III, J. S. BECKETT, A. C. JONES, AND J. M. MASON, JR.
1973. Estimation of rates of tag shedding by northwest Atlantic bluefin tuna. Fish. Bull., U.S. 71:1103-1105.

RAYMOND E. BAGLIN, JR.

Southeast Fisheries Center Miami Laboratory
National Marine Fisheries Service, NOAA, Miami, Fla.
Present address: *National Marine Fisheries Service, NOAA*
c/o Alaska Department of Fish and Game
P.O. Box 686, Kodiak, AK 99615

MARK I. FARBER

Southeast Fisheries Center Miami Laboratory
National Marine Fisheries Service, NOAA
75 Virginia Beach Drive, Miami, FL 33149

WILLIAM H. LENARZ

Southwest Fisheries Center Tiburon Laboratory
National Marine Fisheries Service, NOAA
3150 Paradise Drive, Tiburon, CA 94920

JOHN M. MASON, JR.

Woods Hole Oceanographic Institution, Woods Hole, Mass.
Present address: *Mid-Atlantic Fishery Management Council*
Federal Building, North and New Streets
Dover, DE 19901

INFLUENCE OF LITTLE GOOSE DAM ON UPSTREAM MOVEMENTS OF ADULT CHINOOK SALMON, *ONCORHYNCHUS TSHAWYTSCHA*

A major environmental and economic concern in the Pacific Northwest is the continuing decline in the numbers of Columbia and Snake River salmonids. Several investigators (Johnson 1960 and others) have used biotelemetry to study effects of hydroelectric dams (Figure 1) on the upstream movements of adult salmonids. Results indicated upstream movements were delayed at Bonneville (Schoning and Johnson[1]; Monan and Liscom[2, 3, 4, 5]),

[1]Schoning, R. W., and D. R. Johnson. 1956. A measured delay in the migration of adult chinook salmon at Bonneville Dam on the Columbia River. Fish. Comm. Oreg., Contrib. No. 23, 16 p.

[2]Monan, G. E., and K. L. Liscom. 1971. Final report, radio tracking of adult spring chinook salmon below Bonneville Dam,

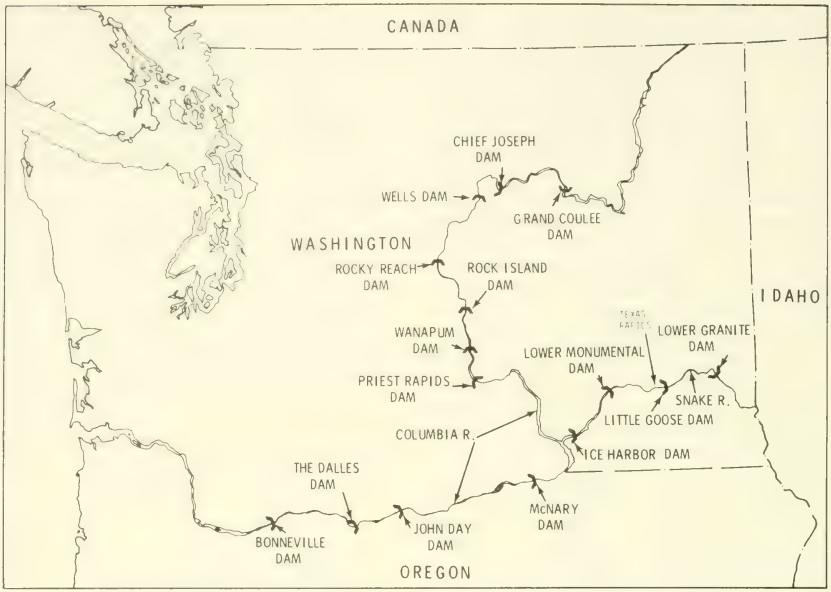


FIGURE 1.—Location of Columbia and Snake River hydroelectric dams.

the Dalles (Monan and Liscom see footnote 3), and Rock Island (French and Wahle 1956) Dams on the Columbia River and at Lower Monumental (Monan and Liscom[6]; Gray and Haynes[7]) and Lower Granite (Liscom and Monan[8]) Dams on the Snake River. However, delays of upstream migrants were generally not considered excessive. We used radiotelemetry to evaluate effects of Little Goose Dam on upstream movements of chinook salmon, *Oncorhynchus tshawytscha*, in the lower Snake River, and compared our results with those of previous studies at other dams.

Materials and Methods

Our telemetry equipment was developed at the Bioelectronics Laboratory, University of Minnesota (Tester and Siniff[9]; Winter et al.[10]). Transmitters were pressure-sensitive and permitted determination of salmon location and swim-

1971. Northwest Fisheries Center, Natl. Mar. Fish. Serv., NOAA, Seattle, Wash., 24 p.

[3]Monan, G. E., and K. L. Liscom. 1973. Final report, radio tracking of adult spring chinook salmon below Bonneville and the Dalles Dams, 1972. Northwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, 37 p.

[4]Monan, G. E., and K. L. Liscom. 1974. Radio tracking studies of fall chinook salmon to determine effect of peaking on passage at Bonneville Dam, 1973. Northwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, 28 p.

[5]Monan, G. E., and K. L. Liscom. 1975. Final report, radio tracking studies to determine the effect of spillway deflectors and fallback on adult chinook salmon and steelhead trout at Bonneville Dam, 1974. Northwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, 38 p.

[6]Monan, G. E., and K. L. Liscom. 1974. Final report, radio tracking of spring chinook salmon to determine effect of spillway deflectors on passage at Lower Monumental Dam, 1973. Northwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, 20 p.

[7]Gray, R. H., and J. M. Haynes. 1976. Upstream movement of adult salmonids in relation to gas supersaturated water. *In* Pacific Northwest Laboratory Annual Report for 1975, p. 73-76. Vol. I, Life Sciences, Part 2, Ecological Sciences. Battelle, Pacific Northwest Laboratories, Richland, Wash.

[8]Liscom, K. L., and G. E. Monan. 1976. Final report, radio tracking studies to evaluate the effects of the spillway deflectors at Lower Granite Dam on adult fish passage, 1975. Northwest Fish. Cent., Natl. Mar. Fish Serv., NOAA, Seattle, 18 p.

[9]Tester, J. R., and D. B. Siniff. 1976. Vertebrate behavior and ecology progress report for period July 1, 1975-June 30, 1976. COO-1332-123. Prepared for U.S. Energy Research and Development Administration. Contract No. E(11-1)-1332. University of Minnesota, Minneapolis, 63 p.

[10]Winter, J. D., V. B. Kuechle, D. B. Siniff, and J. R. Tester. 1978. Equipment and methods for radio tracking freshwater fish. Univ. Minn. Agric. Exp. Stn. Misc. Rep. 152-1978, 18 p.

ming depth (Gray and Haynes 1977). Transmitters were individually identifiable and operated on a carrier frequency of 53 MHz. Transmitter range varied with depth and transmitter orientation to a receiving antenna. Transmitter life was 2-3 wk. Receivers were capable of distinguishing 100 discrete crystal-tuned transmitters.

Transmitters used in spring 1976 weighed about 68 g in water and were 11.5 cm long and 2.7 cm in diameter. Transmitters used in 1977 were about one-half the weight and two-thirds the volume of those used initially, weighed about 34 g in water, and were 7.9 cm long and 1.9 cm in diameter. In spring 1976 and 1977, chinook salmon were trapped, anesthetized (tricaine methanesulfonate-quinaldine), and tagged externally with radio and metal-core anchor tags (experimental) or metal-core anchor tags only (controls). Tagging was accomplished in cooperation with the National Marine Fisheries Service (NMFS) at Little Goose Dam. Methods of external tag attachment were reported by Gray and Haynes (1977). After tagging, salmon were transported 6.4 km downstream and released at Texas Rapids (Figure 1).

Total lengths and weights of tagged salmon ranged from 66 to 100 cm and 3.4 to 11.4 kg and were consistent with the sizes of fish used in other Columbia River studies (Monan and Liscom see footnotes 2-6). Fish movements between Lower Monumental and Lower Granite Dams (Figure 1) were monitored day and night for the duration of transmitter life. Tagged fish passing through fish ladders at Little Goose and Lower Granite Dams were automatically diverted into fish traps by a magnetometer-triggered device (Durkin et al. 1969), or observed and recorded at fish-counting windows. This allowed comparison of travel time data for control and experimental fish. Total distance traveled was calculated for each fish by summing movements between successive locations.

Results and Discussion

Extensive timing variability among individual salmon was common throughout the study. However, travel times of salmon carrying external radio transmitters and control fish were not significantly different (Gray and Haynes 1979). Average passage delays at Little Goose Dam for radio-tagged and control salmon (combined) were 216 ± 210 h ($n = 45$) in 1976 and 90 ± 57 h ($n = 48$) in 1977 (Table 1). Passage delays for the same fish at Lower Granite Dam were $< 50 \pm 19$ h ($n = 3$) in 1976 and 58 ± 45 h ($n = 18$) in 1977.

While our observations of delay at Lower Granite Dam were consistent with previous research at other Columbia and Snake River Dams (Table 1), it appears that excessive delays occurred at Little Goose Dam, especially in 1976. Differences in passage times at Little Goose Dam compared with other dams (Table 1) were significant ($P < 0.05$, Mann-Whitney test).

Several observations indicate extensive salmon

TABLE 1.—Delay of tagged adult chinook salmon below Columbia and Snake River Dams.

Dam	Study year(s)	Citation	Tag type[1]	No. of fish	Time[2] (h) Mean	Range
Bonneville	1948	Schoning and Johnson (text footnote 1)	NT	35	67	62-72
Bonneville	1971	Monan and Liscom (text footnote 2)	R	20	[3] 63	4-86
Bonneville	1972	Monan and Liscom (text footnote 3)	R	20	141	11-408
Bonneville	1973	Monan and Liscom (text footnote 4)	R	52	[4] 96	24-384
Bonneville	1974	Monan and Liscom (text footnote 5)	R	42	54	3-540
The Dalles	1972	Monan and Liscom (text footnote 3)	R	30	33	4-69
Rock Island	1954-56	French and Wahle (1956)	NT	2,217	72	48-96
Lower Monumental	1973	Monan and Liscom (text footnote 6)	R	20	62	—
Lower Monumental	1975	Gray and Haynes (text footnote 7)	R	20	18	2-42
Little Goose	1975	Gray and Haynes (text footnote 7)	R	10	139	20-288
Little Goose	1976	This study	R, NT	45	216	44-858
Little Goose	1977	This Study	R, NT	48	90	23-212
Lower Granite	1975	Liscom and Monan (text footnote 8)	R	30	78	—
Lower Granite	1976	This study	R	3	< 50	35-72
Lower Granite	1977	This study	R	18	58	2-145
Average passage delays, h:						
Little Goose Dam					148.3 ± 63.5	
Other dams					66.0 ± 31.0	
All dams					82.5 ± 49.9	

[1] R = radio transmitter; NT = nontelemetering fish tag.
[2] Values averaged over all fish used in a study.
[3] Time spent in fish ladders only.
[4] Time from release 6.4 km downstream to dam passage.

delays occurred below Little Goose Dam. Radio-tagged salmon travelled mean distances of 26.5 km in 1976 and 42.0 km in 1977 before crossing Little Goose Dam, despite its location only 6.4 km above the Texas Rapids release site. Dropbacks after arrival of fish in the Little Goose Dam spill were common, averaging 1 or 2/fish. Delay times and distances ranged up to 100 h and 40 km/dropback episode. Radio-tagged (1976-77) salmon exhibited three movement patterns after release at Texas Rapids until arrival at Little Goose Dam: 31% (12/39) moved to the dam within 4 to 12 h; 31% (12/39) remained within ±5 km of the release point overnight and moved to the dam the next day; and 38% (15/39) moved downstream as far as 32 km, and then upstream to the dam 1-6 days later.

Once an individual salmon began moving upstream, it traveled 2-5 km/h and, generally, did not stop until reaching Little Goose Dam. After entry into the dam spill, three behavior patterns were observed: 34% (12/35) crossed the dam 2-5 days after release without dropping back; 40% (14/35) crossed the dam after averaging 1.6 dropbacks/fish; and 26% (9/35) were not observed or recorded crossing Little Goose Dam. However, at least four salmon in the latter group were observed passing Lower Granite Dam or were recovered upstream by anglers or at hatcheries, and properly belong in the second group.

At Little Goose Dam, especially with continuous spring 1976 spilling, salmon appeared "confused." Movements to and from the spill area were common. Substantial milling, previously reported at Lower Granite Dam (Liscom and Monan see footnote 8), occurred in a large back eddy on the north side of Little Goose Dam in 1976 and in front of turbine outflows in 1977. Salmon may use rheotactic, olfactory and/or acoustical cues to navigate upstream (Harden Jones 1968). These cues may be distorted by continuous and heavy spilling near dams. Milling may be an attempt to relocate orientation cues (Hasler et al. 1978). In both study years movements into the fish ladder were frequent, but salmon frequently fell back and returned to the spilling basin, especially upon nearing the trapping facility in midladder.

Periodically, fish trapping operations were halted to allow large groups of salmon, which were suspected of accumulating in the spill to pass Little Goose Dam (Slatick[11]). From 26 April to 30 May 1977, the trap was inoperative 17% of the time (6 of 35 days). However, 30% of all salmon counted (7,382 of 24,238) at the fish viewing window by NMFS personnel and 59% (16/27) of our tagged salmon crossed Little Goose Dam during nontrapping periods. Daily viewing window counts of salmon passage averaged 562±497 fish during trapping and 1,230±1,040 fish during nontrapping periods. A t-test showed these differences were significant ($P<0.05$) and indicated trapping operations at Little Goose Dam impeded chinook salmon passage.

Other aspects of dam operations affected salmon passage at Little Goose Dam. One morning in May 1976, spillways were closed for several hours. The five radio-tagged salmon present left the spill and moved downstream as far as 16 km. During the 24 h after spilling was restored, fish returned to the dam. In the absence of spilling in spring 1977, radio-tagged salmon moved into turbulent areas created by water leaving power generating turbines at Little Goose and Lower Granite Dams. When turbine operations were altered, in response to power generation demands, salmon generally exited the area and returned after water-flow conditions stabilized. Salmon passage through the fish ladder was also impeded by turbine operations (Slatick see footnote 11). Finally, the fish ladder at Little Goose Dam uses pumped river water rather than a gravity flow. Of all salmonid species studied, chinook salmon may be most sensitive to and least likely to swim through pumped water (Slatick see footnote 11).

Gray and Haynes (1977) showed that mean swimming depths of adult chinook salmon in the Snake River were significantly greater ($P<0.05$) in spring 1976 than in spring 1977. However, in both years, mean swimming depths in the Little Goose Dam spill were significantly greater ($P<0.05$) than in all other sections of the study area (Haynes 1978). In contrast, swimming depths in the Lower Granite Dam spill were similar to those in the open river between dams. As delays increased in the Little Goose Dam spill, salmon swimming depths increased. Since fish ladder entrances are near the surface, this decreased opportunities for passage.

Although some delays may have resulted from tagging, we believe other factors caused the extensive delays observed at Little Goose Dam. First, our radio-tagged and control salmon had similar passage times at Little Goose and Lower Granite

[11]E. Slatick, National Marine Fisheries Service, Little Goose Dam, Starbuck, Wash., pers. commun. 1977.

Dams in 1976 and 1977 (Gray and Haynes 1979). Second, the 63% passage of internally radio-tagged salmon in 113 h observed by Liscom and Monan (see footnote 8) at Lower Granite Dam was similar to the 69% passage of radio-tagged salmon in 106 h that we observed in spring 1977 for fish that crossed Little Goose Dam or were initially released above it (Haynes 1978).

Our studies provide the first information on salmon movements near Little Goose Dam. Although they affected salmon movements, spilling and turbine operations are regular events at all dams and would not appear to be solely responsible for excessive delays occurring at Little Goose Dam. Fish passage delays may have resulted from tagged salmon being forced to retravel a portion of their migratory route after release. However, tagging and transport stresses, per se, are common to all tagging studies. Our salmon (1976-77) moved to Little Goose Dam in an average of 38 h, a figure consistent with similar studies at Bonneville Dam (Monan and Liscom see footnotes 2-5). Thus, our tagging and handling methods would not appear to be responsible for extensive delays of salmon movements upstream.

Dropback and milling of radio-tagged salmon in the Snake River at Little Goose Dam may be related to salmon trapping operations. Two factors that may contribute to trapping effects are the mechanical aspects of the trap itself and the possible olfactory sensing of trapped salmon by other salmon moving up the fish ladder. Trap entrances are narrow and steep, the trap emits sharp noises when operating, and hydraulic fluid may reach the fish ladder. It is well known that a human hand in the water of a fish ladder can interrupt salmon movement. Many authors (Hasler et al. 1978) have demonstrated great olfactory sensitivity among salmon. The presence of trapped salmon upstream and other disturbances may inhibit salmon passage through fish ladders.

Extensive passage delays, due to dropback and milling and greater swimming depths in the spill below the dam indicate a unique effect of Little Goose Dam on the upstream migration of chinook salmon. We observed delays at Little Goose Dam averaging 148±64 h (Table 1). Delays reported at other dams were significantly less ($P<0.05$) and averaged only 66±31 h. Cause for great concern is the 83±50 h average delay salmon encounter at each dam while migrating through the Columbia and Snake Rivers. Many salmon must pass eight dams (Figure 1) to reach home spawning areas, and the additive effects of a 4 wk, multidam passage delay may significantly influence spawning success, especially in fall run chinook salmon which have shown the greatest decline in numbers. From 1962 to 1969, before Little Goose Dam was operational, annual passage of fall chinook salmon at Ice Harbor Dam averaged nearly 18,000 fish (U.S. Army Corps of Engineers[12]). However, in 1976 and 1977 fall chinook salmon passage at Ice Harbor Dam was only 1,474 and 1,956 fish (U.S. Army Corps of Engineers[13, 14]). Little Goose Dam is 95 km upriver from Ice Harbor Dam (Figure 1). Since the position of fishways, navigation locks, and spillways is different at each dam, effects of each dam must be studied independently. Only then can methods be devised to increase passage success throughout the river system.

Acknowledgments

We thank C. D. Becker and the reviewers of the *Fishery Bulletin* who criticized the manuscript and made substantial contributions to its content; D. W. Crass, S. W. Cubberly, D. D. Dauble, R. W. Hanf, Jr., J. C. Montgomery, and R. P. Olson, who assisted data collection in the field; and G. E. Monan, Northwest and Alaska Fisheries Center, NOAA, Seattle, Wash., and E. Slatick, Little Goose Dam, Starbuck, Wash., who kindly provided information on National Marine Fisheries Service telemetry studies and operational features of Little Goose Dam. The study was supported by the U.S. Department of Energy under Contract EY-76-C-06-1830 with Pacific Northwest Laboratory, operated by Battelle Memorial Institute.

Literature Cited

DURKIN, J. T., W. J. EBEL, AND J. R. SMITH.
1969. A device to detect magnetized wire tags in migrating adult coho salmon. J. Fish. Res. Board Can. 26:3083-3088.

FRENCH, R. R., AND R. J. WAHLE.
1965. Study of loss and delay of salmon passing Rock Island Dam, Columbia River, 1954-56. U.S. Fish. Wildl. Serv., Fish. Bull. 65:339-368.

[12]U.S. Army Corps of Engineers. 1969. Annual Fish Passage Report, Columbia and Snake River Projects, North Pacific Division. Portland and Walla Walla Districts.

[13]U.S. Army Corps of Engineers. 1976. Annual Fish Passage Report. Columbia and Snake River Projects, North Pacific Division. Portland and Walla Walla Districts.

[14]U.S. Army Corps of Engineers. 1977. Annual Fish Passage Report. Columbia and Snake River Projects, North Pacific Division. Portland and Walla Walla Districts.

GRAY, R. H., AND J. M. HAYNES.
1977. Depth distribution of adult chinook salmon (*Oncorhynchus tshawytscha*) in relation to season and gas-supersaturated water. Trans. Am. Fish. Soc. 106:617-620.
1979. Spawning migration of adult chinook salmon (*Oncorhynchus tshawytscha*) carrying external and internal radio transmitters. J. Fish. Res. Board Can. 36:1060-1064.
HARDEN JONES, F. R.
1968. Fish migration. Edward Arnold Publ., Lond., 325 p.
HASLER, A. D., A. T. SCHOLZ, AND R. M. HORRALL.
1978. Olfactory imprinting and homing in salmon. Am. Sci. 66:347-355.
HAYNES, J. M.
1978. Movement and habitat studies of chinook salmon and white sturgeon. Ph.D. Thesis, Univ. Minnesota, Minneapolis, 168 p.
JOHNSON, J. H.
1960. Sonic tracking of adult salmon at Bonneville Dam, 1957. U.S. Fish Wildl. Serv., Fish. Bull. 60:471-485.

JAMES M. HAYNES

Department of Biological Sciences
State University College
Brockport, NY 14420

ROBERT H. GRAY

Freshwater Sciences, Ecosystems Department
Battelle, Pacific Northwest Laboratories
Richland, WA 99352

MATURITY, SPAWNING, AND FECUNDITY OF ATLANTIC CROAKER, *MICROPOGONIAS UNDULATUS*, OCCURRING NORTH OF CAPE HATTERAS, NORTH CAROLINA

The Atlantic croaker, *Micropogonias undulatus*, is an important inshore, bottom fish ranging from the Gulf of Maine to Bay of Campeche, Mexico (Chao 1978). United States commercial landings have reached 50,000 metric tons (t) in recent years (Gutherz et al. 1975; McHugh 1977), though dramatic declines in landings have occurred; at least in the area from Cape Hatteras, N.C., to Cape Cod, Mass. (Joseph 1972). White and Chittenden (1977) have postulated the existence of an abrupt change in life histories and population dynamics of Atlantic croaker and other species whose ranges traverse Cape Hatteras. They showed differences in spawning times, size at maturity, maximum size and age, and total annual mortality rates of Atlantic croakers from north and south of Cape Hatteras and speculated the differences may result from different temperature regimes.

Few studies exist on reproduction of Atlantic croaker occurring north of Cape Hatteras. Wallace (1940) studied size at maturity and sexual development of fish from Chesapeake Bay and ocean waters off Virginia and North Carolina. Welsh and Breder (1923) reported size and age at maturity based on collections from Massachusetts to Florida. Occurrence of larval stages and gonad development indicated that spawning occurred from July through December and peaked during October and November (Welsh and Breder 1923; Hildebrand and Schroeder 1928; Wallace 1940). Haven (1957) and Chao and Musick (1977) found indications from juvenile length frequencies of late winter or early spring spawning. The only report of fecundity was that a 395 mm female contained approximately 180,000 eggs (Hildebrand and Schroeder 1928).

This paper presents size at maturity, spawning times as indicated by ovarian development, and fecundity observations of the Atlantic croaker population north of Cape Hatteras.

Methods

All fish were collected during seven National Marine Fisheries Service bottom-trawl surveys of the continental shelf from Cape Hatteras to Block Island, R.I., during 1973-76 (Table 1). The survey design and sampling methods were described by Grosslein (1969). Atlantic croakers were captured each year between lat. 39°00′ N (Cape May, N.J.) and 35°15′ N (Cape Hatteras) in depths from 7 to 131 m.

Subsamples of approximately 25 fish, representative of the length frequency of each catch, were frozen whole for laboratory examination. Each fish was weighed (grams), measured (millimeters total length, TL), sexed, and its maturity stage was determined using the sexual development classification and criteria of Wallace (1940).

TABLE 1.—Summary of Atlantic croaker data collected between Cape May, N.J., and Cape Hatteras, N.C., during 1973-76.

Collection no.	Dates	No. of observations	Number used in probit analysis	
			Males	Females
1	9-16 Oct. 1973	556	245	286
2	27-30 Sept. 1974	699	324	258
3	16-18 Sept. 1975	79	31	28
4	30 Oct.-6 Nov. 1975	607	204	145
5	14-17 Dec. 1975	122	—	—
6	6-17 Oct. 1976	438	84	103
7	18 Dec. 1976	16	—	—
Total		2,517	888	820

Ovaries in development stage 4 from 1973 and 1974 cruises were exsected, weighed (±0.01 g), and preserved in a modified Gilson's fluid (Simpson 1951) for subsequent fecundity estimation.

Egg counts for fecundity estimation were made by a method similar to Bagenal's (1957), but modified as follows. After 4-6 wk preservation the ovaries were washed over a 1.0 mm mesh screen which permitted all the eggs to pass through it but retained the ovarian tissue. After repeated washings and decanting the eggs were diluted in water to a known volume, randomly stirred, and three 10 ml aliquots, each containing from 200 to 400 eggs, were extracted and the eggs counted using a microscope. To test the accuracy of the sampling method two aliquots were extracted from an egg batch, counted, and replaced until 20 aliquots were counted. The mean and standard deviation (SD) of all counts was 255 and 38.3, and the coefficient of variation (CV) was 15.0%. For the means of three samples the SD was 20.4 and the CV was 8.7%. The mean egg number of the three aliquots times the total dilution volume divided by the aliquot volume was used to estimate fecundity.

Estimates of length at maturity (length at which 50% are mature = L_{50}) were calculated using probit analysis (Finney 1971). Samples used in this analysis were collected from September to November (Table 1; cruises 1-4, 6) which minimizes the affects of seasonal growth on length at maturity. The proportion of mature fish for each centimeter group was calculated for each year by sex. Table 2 shows the proportion mature by centimeter group for the interval between 0 and 100% mature. The proportions were transformed to probits (Fisher and Yates 1964) and the iterative method was used to calculate the weighted linear regression equation, $Y = a + b\,X$, by least squares for the logarithm (base 10) of length (X) and the probit (Y). Chi-square tests indicated no significant ($\chi^2_{0.01}$) heterogeneous deviations from the regression lines; therefore, the regression coefficients were used to determine L_{50}. The variance of L_{50} was estimated as:

$$V(L_{50}) = \frac{1}{b^2}\left[\frac{1}{\Sigma nw} + \frac{\left(L_{50} - \frac{\Sigma nwx}{\Sigma nw}\right)^2}{\Sigma nw\left(x - \frac{\Sigma nwx}{\Sigma nw}\right)^2}\right]$$

where n is the number of observations at each centimeter group, w is the weighting coefficient (Z^2/PQ) (Finney 1971, table II) for probit (Y), and x is the logarithm (base 10) of the length.

In order to test for differences in L_{50} between sexes and between years, z-values (Natrella 1966) were calculated using the equation:

$$z = \frac{L_{50_1} - L_{50_2}}{\sqrt{V(L_{50_1}) + V(L_{50_1})}}\ .$$

TABLE 2.—Percentage mature used in probit analysis by total length group for male (M) and female (F) Atlantic croaker collected in 1973-76. N = number of specimens, L_{50} = length at 50% mature, $V(L_{50})$ = variance of L_{50}, and χ^2 = for goodness of fit of probit regression line.

Total length (cm)	1973		1974		1975		1976	
	M	F	M	F	M	F	M	F
16							0	
17		0			0		17	0
18	0	10	0		16	0	13	31
19	17	29	9	0	18	10	67	70
20	69	45	36	10	37	33	89	80
21	90	86	47	23	32	28	91	85
22	94	84	56	35	47	30	90	83
23	89	78	65	47	50	27	100	71
24	92	86	85	74	47	43		94
25	97	94	95	93	78	69		100
26	100	97	98	97	77	79		
27		100	100	100	90	82		
28					93	100		
29					100			
N	245	286	324	258	235	173	84	103
L_{50}	19.17	19.81	21.57	22.70	22.35	23.27	18.71	18.52
$V(L_{50})$	0.0190	0.0191	0.0357	0.0283	0.0376	0.0356	0.0438	0.0234
χ^2	15.82	13.82	5.11	3.97	7.07	12.16	4.09	8.66
df	7	9	8	7	11	9	6	7

Results and Discussion

Length at Maturity

The matrix of z-values is shown in Table 3. Highly significant ($z>2.33$, $P\leq 0.01$) differences were found between sexes within years for 1975 and 1976 and between years for each sex except 1973 and 1976 males and 1974 and 1975 females. This indicates that L_{50} for males and females was greater in 1974 and 1975 than in 1973 and 1976. The greatest difference was found between 1975 and 1976 when L_{50} decreased approximately 4.8 cm for females and 3.6 cm for males.

Significant long-term changes in L_{50} have occurred since Wallace's (1940) studies of Chesapeake Bay croakers. The smallest mature female he observed during 1938-40 was 27.5 cm, indicating a L_{50} of at least 30 cm. His collections were made during July and August; therefore, due to additional growth during early fall, 30 cm is an underestimation of L_{50} for comparison with my results obtained from September-November.

Spawning

The percentage frequencies of maturity stages indicate spawning commenced at least as early as the beginning of September, peaked during October, and ended by late December. The maturity stages and sample years were combined for analysis (Table 4). The percentage of ripe ovaries remained high during September and October, then dropped to a low level in November. No ripe females were found in December. As would be expected the percentage of spawned fish (partially spent, spent, and resting) increased during the sampling period and indicated spawning was nearly completed by mid-December. Because of difficulty in assigning a specific maturity stage to testes and since ovarian development was the best indicator of spawning, males were not analyzed.

The beginning of the spawning season was not sampled; however, an examination of Wallace's (1940) maturity stage data for July and August showed that over 50% of the ovaries were developing (stages II and III) and <10% were ripe (stage IV). The remainder was classified as resting (stage I). Wallace made additional collections in November which showed that ovaries were either partially spent (stage VI) or spent (stage VII). His findings support this study, indicating that spawning commenced about mid-August and was completed by the end of December.

The presence of small juveniles (20-40 mm TL) during April and May have led to speculations of different spawning populations and a spring spawning peak. Chao and Musick (1977) apparently detected a modal group "entering" the York River in May and suggested they may represent

TABLE 3.—Matrix of z-values (Natrella 1966) and significance for differences in L_{50} (length at which 50% of specimens were mature) of male (M) and female (F) Atlantic croaker collected in 1973-76.

	1973		1974		1975		1976	
	M	F	M	F	M	F	M	F
1973 M		0.196	7.269**	16.214**	9.632**	17.546**	6.937**	5.779**
F				9.058**		7.544**		3.196**
1974 M				4.467**	2.903*	6.367**	6.329**	12.546**
F						1.400		12.122**
1975 M						3.400**	8.055**	15.507**
F								9.972**
1976 M								0.729

*$P<0.01$. **$P<0.001$.

TABLE 4.—Percentage frequency of maturity stages of female Atlantic croaker collected between Cape May, N.J., and Cape Hatteras, N.C., during 1973-76.

		Sampling interval				
Maturity stage	Wallace's stages (1940)	16-18 Sept. 1975	29 Sept.-1 Oct. 1974	5-20 Oct. 1973, 1976	30 Oct.-6 Nov. 1975	14-17 Dec. 1975
Developing	II and III	51	29	23		
Ripe	IV and V	46	51	41	12	
Partially spent	VI	3	7	13	31	10
Spent	VII		11	17	32	28
Resting	I		2	6	25	62
Total		42	286	448	196	51

progeny from a different spawning population. Haven (1957) found 20-30 mm fish during April and concluded the spawning season extended over almost the entire year with a possible spring peak. The apparent 9- or 10-mo spawning season may result from little or no overwinter growth or sampling bias due to differential size distribution or trawl avoidance (Haven 1957; White and Chittenden 1977; Chao and Musick 1977). Maturity observations made during this study showed essentially all adult fish spawned during August through December and it is unlikely a spring spawning peak would occur from the Atlantic croaker population north of Cape Hatteras.

Fecundity

Fecundity ranged from 100,800 to 1,742,000 for fish from 196 to 390 mm TL. Preliminary plots of fish length versus fecundity indicated a curvilinear relationship and plots of fish weight and ovary weight versus fecundity appeared linearly related. Therefore, fish length and fecundity were transformed to logarithms (base 10) and least squares regression lines fitted to the data by year using the equation log fecundity = $\log a + b$ (log length). Fish weight and ovary weight versus fecundity were related by the linear regression equation $Y = a + bX$ where Y is fecundity and X is either fish weight or ovary weight. Analysis of variance indicated no significant ($P \leq 0.05$) differences in variance about the regression between years for each of fecundity versus length, weight or ovary weight. Analysis of covariance was used to test for between years differences in fecundity relationship. No significant ($P = 0.01$) difference was indicated; therefore, regression equations were calculated for pooled data. Scatter diagrams and fitted lines are shown in Figures 1-3.

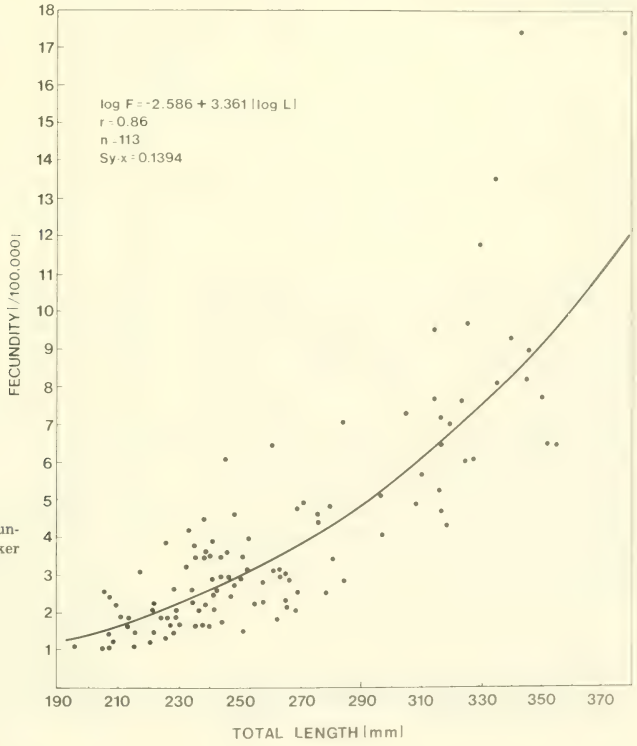


FIGURE 1.—Relationship between fecundity and total length for Atlantic croaker collected in 1973 and 1974.

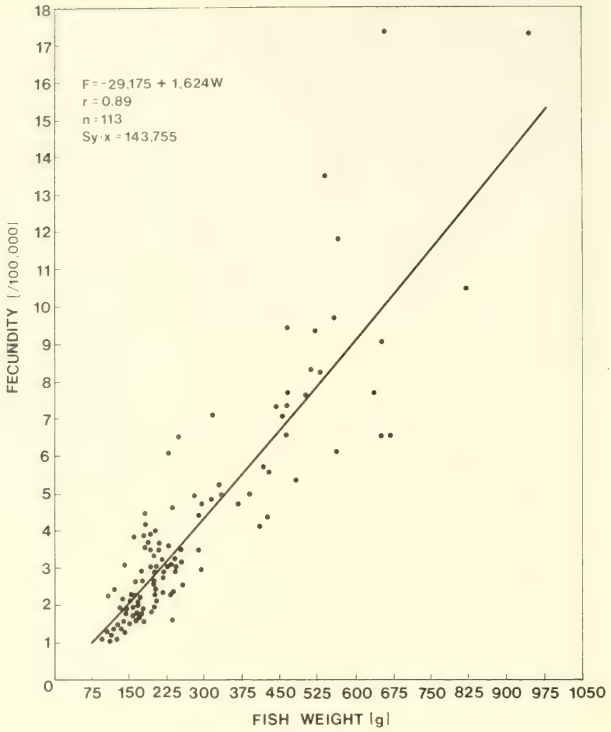


FIGURE 2.—Relationship between fecundity and fish weight for Atlantic croaker collected in 1973 and 1974.

The correlation coefficients for the relationships of fecundity to length, weight, and ovary weight show ovary weight was most closely associated with the variation of fecundity. Unless the ovaries are selected, however, ovary weight is the least reliable predictor of fecundity. It is the most variable parameter and, unless ovaries are collected at the penultimate development stage, the relationship of ovary weight and fecundity will vary seasonally. Fish weight will also vary seasonally and, when ovary weight is included with fish weight, some autocorrelation is present. For general prediction of fecundity, length appears to be the most reliable measure.

Acknowledgments

I wish to thank the many people who helped collect samples during National Marine Fisheries Service cruises and S. J. Wilk and W. G. Smith for their critical reviews of early drafts. Special thanks to M. Montone for her assistance and typing of this manuscript and to M. Cox for preparation of the figures.

Literature Cited

BAGENAL, T. B.
1957. The breeding and fecundity of the long rough dab *Hippoglossoides platessoides* (Fabr.) and the associated cycle in condition. J. Mar. Biol. Assoc. U.K. 36:339-375.

CHAO, L. N.
1978. A basis for classifying western Atlantic Sciaenidae (Teleostei: Perciformes). U.S. Dep. Commer., NOAA Tech. Rep. NMFS Circ. 415, 64 p.

CHAO, L. N., AND J. A. MUSICK.
1977. Life history, feeding habits, and functional morphology of juvenile sciaenid fishes in the York River estuary, Virginia. Fish. Bull., U.S. 75:657-702.

FINNEY, D. J.
1971. Probit analysis. 3d ed. Camb. Univ. Press, Lond., 333 p.

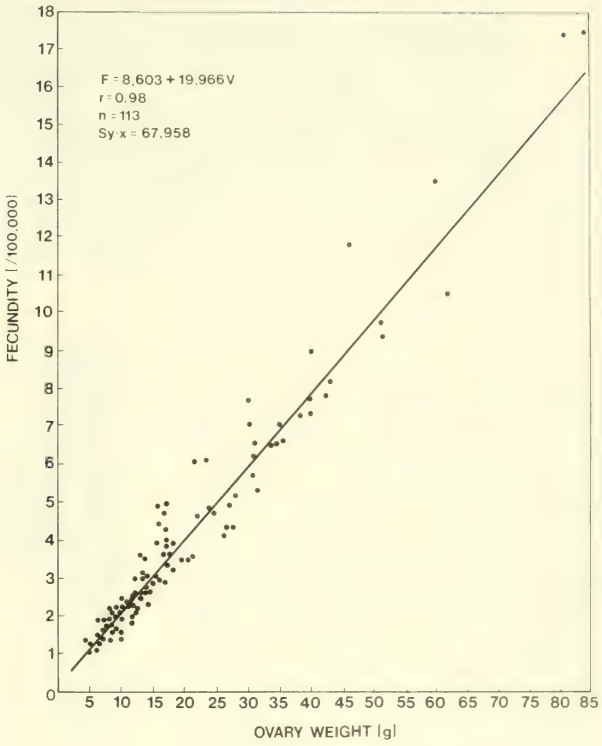


FIGURE 3.—Relationship between fecundity and ovary weight for Atlantic croaker collected in 1973 and 1974.

FISHER, R. A., AND F. YATES.
1964. Statistical tables for biological, agricultural and medical research. 6th ed. Oliver and Boyd, Edinb., 146 p.

GROSSLEIN, M. D.
1969. Groundfish survey program of BCF Woods Hole. Commer. Fish. Rev. 31(8-9):22-30.

GUTHERZ, E. J., G. M. RUSSELL, A. R. SERRA, AND B. A. ROHR.
1975. Synopsis of the northern Gulf of Mexico industrial and food fish industries. Mar. Fish. Rev. 37(7):1-11.

HAVEN, D. S.
1957. Distribution, growth, and availability of juvenile croaker, *Micropogon undulatus*, in Virginia. Ecology 38:88-97.

HILDEBRAND, S. F., AND W. C. SCHROEDER.
1928. Fishes of Chesapeake Bay. Bull U.S. Bur. Fish. 43(1), 366 p.

JOSEPH, E. B.
1972. The status of the sciaenid stocks of the middle Atlantic coast. Chesapeake Sci. 13:87-100.

MCHUGH, J. L.
1977. Fisheries and fishery resources of New York Bight. U.S. Dep. Commer., NOAA Tech. Rep. NMFS Circ. 401, 50 p.

NATRELLA, M. G.
1963. Experimental statistics. U.S. Dep. Commer., Natl. Bur. Stand. Handb. 91, 528 p.

SIMPSON, A. C.
1951. The fecundity of the plaice. Fish. Invest. Minist. Agric. Fish. Food (G.B.) Ser. II, 17(5), 27 p.

WALLACE, D. H
1940. Sexual development of the croaker, *Micropogon undulatus*, and distribution of the early stages in Chesapeake Bay. Trans. Am. Fish. Soc. 70:475-482.

WELSH, W. W., AND C. M. BREDER, JR.
1923. Contributions to life histories of Sciaenidae of the eastern United States coast. Bull. U.S. Bur. Fish. 39:141-201.

WHITE, M. L., AND M. E. CHITTENDEN, JR.
1977. Age determination, reproduction, and population dynamics of the Atlantic croaker, *Micropogonias undulatus*. Fish. Bull., U.S. 75:109-123.

WALLACE W. MORSE

Northeast Fisheries Center Sandy Hook Laboratory
National Marine Fisheries Service, NOAA
Highlands, NJ 07732

COMPARISON OF SAMPLING DEVICES FOR THE JUVENILE BLUE CRAB, *CALLINECTES SAPIDUS*[1]

The behavior of the blue crab, *Callinectes sapidus* Rathbun, in the Chesapeake Bay varies considerably with age, temperature, and molting cycle. These behavioral differences make efforts difficult to sample effectively the population densities in the Chesapeake Bay and its tributaries. No single gear type appears to sample effectively the blue crab during winter and summer at all depths and types of bottom. During winter blue crabs burrow in the mud in the deeper channels of Chesapeake Bay (Churchill 1917). This pattern is the basis for an active winter dredge fishery in the lower portion of the bay (Van Engel 1962). During a 3-yr survey of blue crabs, Lippson[2] found that juveniles were also present in deeper waters in winter. Comparative effectiveness of two dredges for winter sampling of juvenile and adult blue crabs was reported by Sulkin and Miller (1975).

Blue crabs move about in relatively shallow water in warm weather presumably because of the abundance of food here and for protection among submerged aquatics while in the soft shell condition. During the summer 7.3 m otter trawls have been found to be an effective gear to sample the adult population of blue crabs (Lippson see footnote 2). The otter trawl, with a small stretch mesh (0.6 cm) liner in the cod end, is also effective for catching juveniles in deeper water; however, juveniles spend much of their time in shallow waters during the warmer months. The push net (Figure 1), beach seine, and small otter trawls have all been used with some degree of success in this shallow region.

It is the purpose of this study to compare the effectiveness of the push net, otter trawl, and crab scrape (Figure 2) in catching juvenile blue crabs in shallow water.

Methods and Results

Smith Island in the Chesapeake Bay has extensive grassy (*Zostera marina*) beds which are ideal habitats for juvenile crabs (Stevenson and Confer 1978). This region was chosen to compare the catch effectiveness among a 3.7 m otter trawl, 81.3 cm push net, and a 96.5 cm modified crab scrape during summer 1975.

The otter trawl opened to a working width of 3.6 m. The gear was towed by the RV *Chelae* in depths of 1-2 m for 0.7 km. The cod end was lined with 0.6 cm stretch mesh netting. The trawl door size was 30.5 cm × 61.0 cm and the length of the bridle was 45.7 m.

The push net had a steel frame 81.3 cm wide and 60.9 cm high fitted with a 0.6 cm stretch mesh bag. The leading edge had a 7.6 cm diameter pipe which

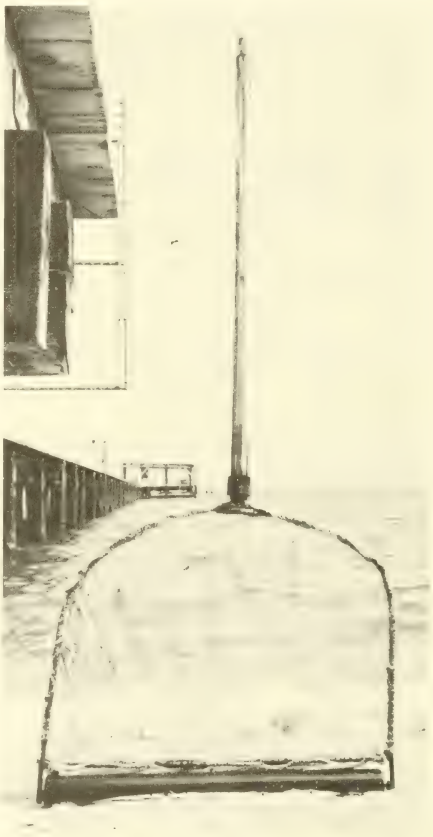


FIGURE 1.—Push net used for blue crab fishing with the roller bar on the leading edge.

[1]Contribution No. 992HPEL from the Center for Environmental and Estuarine Studies, University of Maryland.

[2]Lippson, R. L. 1969. Blue crab study in Chesapeake Bay-Maryland. Nat. Resour. Inst. Q. Prog. Rep. 3, Ref. No. 69-33B:1-13.

FIGURE 2.—The crab scrape used for blue crab fishing.

rolled over the bottom. The handle was 1.5 m long. The net was manually pushed along a 0.7 km course, waist to chest deep, and parallel to the shoreline.

The crab scrape, used commercially for catching shedding crabs, had a metal frame 96.5 cm wide and 38.1 cm high. The lead bar on the crab scrape has no teeth, a basic difference between it and a dredge. A 3.8 cm twine net 182.9 cm long was fitted to this frame. The crab scrape is towed from a shallow-draft boat over grassy beds. The crab scrape used in this study was modified by fitting it with a 0.6 cm stretch mesh net to retain small (>3 mm) crabs.

The otter trawl and crab scrape were towed simultaneously beside each other from two small outboard motorboats for 6 min at an engine speed of 2,000 r/min. The push net was then pushed parallel to the trawl and crab scrape tows over the same distance but closer to shore. The depths for the trawl and crab scrape tows ranged from 1 to 2 m whereas the push net sampled in depths of 0.6-1.1 m. Eighteen samples were collected for each gear type.

The sex and size class of crabs were determined after each tow. Crab size was determined using carapace width from one lateral spine tip to the other. Crabs >60 mm wide were excluded from consideration in this study because they were not in the most recent year class. Three size classes were used: class I measured 1 to 20.0 mm; class II, 20.1 to 40.0 mm; and class III, 40.1 to 60.0 mm.

The mean number of crabs per square meter is shown in Figure 3. It is apparent that the trawl is comparatively ineffective for classes I and II. The trawl and push net are about equally as effective for class III although neither is as effective as the modified crab scrape for classes I, II, or III. The crab scrape is the most effective gear for sampling juvenile blue crabs.

FIGURE 3.—Mean number of blue crabs per square meter for each haul and total area fished by each gear. Size class (carapace width) I = 1-20.0 mm, II = 20.1-40.0 mm, and III = 40.1-60.0 mm.

Discussion

In evaluating various gear for sampling juvenile blue crabs, a variety of factors should be considered, such as catch effectiveness, gear cost, ease of handling, and person hours.

It generally requires two persons to efficiently operate an otter trawl from a small outboard motorboat. Handling an otter trawl from a small outboard motorboat is not only difficult but dangerous as the net can become fouled in the propeller. If the net fills with mud or too much debris, it is impossible to bring the gear on board and the catch must be sacrificed. The push net is operable by one person and snags are infrequent. Mud, as well as high rooted aquatics, makes pushing the net difficult. The push net is effective in shallow water (Strawn 1954). Clear shallow water, however, decreases the effectiveness as many small crabs see the net approaching and swim out of its path (pers. obs.). The crab scrape can be easily handled by one person and seldom becomes snagged (pers. obs. and observations of commercial crabbers).

The cost of a 3.7 m otter trawl is about $150.00. The push net cost varies. They are not available commercially and must be constructed, usually by a local blacksmith. The bag may be cut from a ripped beach seine net. The approximate cost of the crab scrape is $55.00.

Although gear cost, ease of handling, and hours involved are considered in gear selection, the most important factor is catch effectiveness. The push net was more effective catching small blue crabs than the trawl but the modified crab scrape was more effective than either the push net or the trawl when sampling in shallow water.

Considering all pertinent factors, it would seem that the crab scrape is the preferred gear for quantitative studies of juvenile crab abundance.

Acknowledgments

We thank Fred Dobbs and Marion Ross for their valuable assistance during the field sampling, Frances Younger for her technical help in the preparation of the graphs, and Leo Minasian and Donna L. Smawley for their photographic assistance. Our thanks are also extended to Nancy Robbins and Ida Marbury for their help in the preparation of the manuscript. This research has been supported by the National Marine Fisheries Service and the State of Maryland Fisheries Administration (Project No. 3-186-R-2, Contract No. 04-5-043-43).

Literature Cited

CHURCHILL, E. P., JR.
1917. Life-history of the blue crab of the Chesapeake Bay. Off. Bull., Conserv. Comm. Md. 2:11-18.

STRAWN, K.
1954. The pushnet, a one-man net for collecting in attached vegatation. Copeia 1954:195-197.

SULKIN, S. D., AND R. E. MILLER.
1975. Modified commercial crab and oyster dredges as sampling devices for the blue crab *Callinectes sapidus* Rathbun. Chesapeake Sci. 16:137-139.

STEVENSON, J. C., AND N. M. CONFER.
1978. Summary of available information on Chesapeake Bay submerged vegatation. U.S. Fish Wildl. Serv., Off. Biol. Serv. FWS/OBS-78/66, 335 p.

VAN ENGEL, W. A.
1962. The blue crab and its fishery in Chesapeake Bay. Part 2 - Types of gear for hard crab fishing. Commer. Fish. Rev. 24(9):1-10.

ROBERT E. MILLER

Horn Point Environmental Laboratories
Center for Environmental and Estuarine Studies
University of Maryland
P.O. Box 775, Cambridge, MD 21613

DOUGLAS W. CAMPBELL
PAMELA J. LUNSFORD

Fisheries Administration
Maryland Department of Natural Resources
Tawes State Office Building
Annapolis, MD 21401

NOTICES

NOAA Technical Reports NMFS published during the last 6 mo of 1979.

Circular

424. Guide to the leptocephali (Elopiformes, Anguilliformes, and Notacanthiformes). By David G. Smith. July 1979, iv + 39 p., 54 fig., 1 app.

425. Marine flora and fauna of the northeastern United States. Arthropoda: Cirripedia. By Victor A. Zullo. April 1979, iii + 29 p., 40 fig., 1 table. For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402 - Stock No. 003-017-00453-8.

426. Synopsis of biological data on the rock crab, *Cancer irroratus* Say. By Thomas E. Bigford. May 1979, v + 26 p., 11 fig., 21 tables. Also FAO Fisheries Synopsis No. 123.

427. Ocean variability in the U.S. Fishery Conservation Zone, 1976. By Julien R. Goulet, Jr. and Elizabeth D. Haynes, editors. July 1979, iv + 362 p.

428. Morphological comparisons of North American sea bass larvae (Pisces: Serranidae). By Arthur W. Kendall, Jr. August 1979, iv + 50 p., 43 fig., 9 tables, 1 app. table.

429. Synopsis of biological data on tunas of the genus *Euthynnus*. By Howard O. Yoshida. October 1979, iv + 57 p., 40 fig., 30 tables. Also FAO Fisheries Synopsis No. 122.

Special Scientific Report—Fisheries

735. History of the fishery and summary statistics of the sockeye salmon, *Oncorhynchus nerka*, runs to the Chignik Lakes, Alaska, 1888-1966. By Michael L. Dahlberg. August 1979, iv + 16 p., 15 fig., 11 tables. For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402 - Stock No. 003-017-00459-7.

736. A historical and descriptive account of Pacific coast anadromous salmonid rearing facilities and a summary of their releases by region, 1960-76. By Roy J. Wahle and Robert Z. Smith. September 1979, iv + 40 p., 15 fig., 25 tables, 2 app. tables. For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402 - Stock No. 003-017-00460-1.

737. Movements of pelagic dolphins (*Stenella* spp.) in the eastern tropical Pacific as indicated by results of tagging, with summary of tagging operations, 1969-76. By W. F. Perrin, W. E. Evans, and D. B. Holts. September 1979, iii + 14 p., 9 fig., 8 tables. For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402 - Stock No. 003-017-00462-7.

738. Environmental baselines in Long Island Sound, 1972-73. By R. N. Reid, A. B. Frame, and A. F. Draxler. December 1979, iv + 31 p., 40 fig., 6 tables. For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402 - Stock No. 003-017-00466-0.

739. Bottom-water temperature trends in the Middle Atlantic Bight during spring and autumn, 1964-76. By Clarence W. Davis. December 1979, iii + 13 p., 10 fig., 9 tables. For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402 - Stock No. 003-017-00467-8.

Most NOAA publications are available by purchase from the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402. Individual copies of NOAA Technical Reports (in limited numbers) are available free to Federal and State government agencies and may be obtained by writing to User Services Branch (D822), Environmental Science Information Center, NOAA, Rockville, MD 20852.

INFORMATION FOR CONTRIBUTORS TO THE *FISHERY BULLETIN*

Manuscripts submitted to the *Fishery Bulletin* will reach print faster if they conform to the following instructions. These are not absolute requirements, of course, but desiderata.

CONTENT OF MANUSCRIPT

The **title page** should give only the title of the paper, the author's name, his affiliation, and mailing address, including ZIP code.

The **abstract** should not exceed one double-spaced page.

In the **text,** *Fishery Bulletin* style, for the most part, follows that of the *U.S. Government Printing Office Style Manual.* Fish names follow the style of the American Fisheries Society Special Publication No. 6, *A List of Common and Scientific Names of Fishes from the United States and Canada,* Third Edition, 1970.

Text footnotes should be typed separately from the text.

Figures and **tables,** with their legends and headings, should be self-explanatory, not requiring reference to the text. Their placement should be indicated in the right-hand margin of the manuscript.

Preferably **figures** should be reduced by photography to 5¾ inches (for single-column figures, allowing for 50% reduction in printing), or to 12 inches (for double-column figures). The maximum height, for either width, is 14 inches. Photographs should be printed on glossy paper.

Do not send original drawings to the Scientific Editor; if they, rather than the photographic reductions, are needed by the printer, the Scientific Publications Office will request them.

Each **table** should start on a separate page. Consistency in headings and format is desirable. Vertical rules should be avoided, as they make the tables more expensive to print. Footnotes in tables should be numbered sequentially in arabic numerals. To avoid confusion with powers, they should be placed to the *left* of numerals.

Acknowledgments, if included, are placed at the end of the text.

Literature is cited in the text as: Lynn and Reid (1968) or (Lynn and Reid 1968). All papers referred to in the text should be listed alphabetically by the senior author's surname under the heading "Literature Cited." Only the author's surname and initials are required in the **literature cited.** The accuracy of the **literature cited** is the responsibility of the author. Abbreviations of names of periodicals and serials should conform to *Biological Abstracts List of Serials with Title Abbreviations. (Chemical Abstracts* also uses this system, which was developed by the American Standards Association.)

Common **abbreviations** and **symbols,** such as mm, m, g, ml, mg, ° C (for Celsius), %, ‰,and so forth, should be used. Abbreviate units of measure only when used with numerals. Periods are only rarely used with abbreviations.

We prefer that **measurements** be given in metric units; other equivalent units may be given in parentheses.

FORM OF THE MANUSCRIPT

The original of the manuscript should be typed, double-spaced, on white bond paper. Please triple space above headings. We would rather receive good duplicated copies of manuscripts than carbon copies. The sequence of the material should be:

TITLE PAGE
ABSTRACT
TEXT
LITERATURE CITED
APPENDIX
TEXT FOOTNOTES
TABLES (Each table should be numbered with an arabic numeral and heading provided)
LIST OF FIGURES (Entire figure legends)
FIGURES (Each figure should be numbered with an arabic numeral; legends are desired)

ADDITIONAL INFORMATION

Send the ribbon copy and two duplicated or carbon copies of the manuscript to:

Dr. Jay C. Quast, Scientific Editor
Fishery Bulletin
Northwest and Alaska Fisheries Center
Auke Bay Laboratory,
National Marine Fisheries Service, NOAA
P.O. Box 155, Auke Bay, AK 99821

Fifty **separates** will be supplied to an author free of charge and 100 supplied to his organization. No covers will be supplied.

Contents–continued

TESTAVERDE, SALVATORE A., and JAMES G. MEAD. Southern distribution of the Atlantic whitesided dolphin, *Lagenorhynchus acutus*, in the western North Atlantic 167
MATARESE, ANN C., and DAVID L. STEIN. Additional records of the sculpin *Psychrolutes phrictus* in the eastern Bering Sea and off Oregon 169
ODELL, DANIEL K., EDWARD D. ASPER, JOE BAUCOM, and LANNY H. CORNELL. A recurrent mass stranding of the false killer whale, *Pseudorca crassidens*, in Florida 171
BRANSTETTER, STEVEN, and ROBERT L. SHIPP. Occurrence of the finetooth shark, *Carcharhinus isodon*, off Dauphin Island, Alabama 177
BAGLIN, RAYMOND E., JR., MARK I. FARBER, WILLIAM H. LENARZ, and JOHN M. MASON, JR. Shedding rates of plastic and metal dart tags from Atlantic bluefin tuna, *Thunnus thynnus* 179
HAYNES, JAMES M., and ROBERT H. GRAY. Influence of Little Goose Dam on upstream movements of adult chinook salmon, *Oncorhynchus tshawytscha* 185
MORSE, WALLACE W. Maturity, spawning, and fecundity of Atlantic croaker, *Micropogonias undulatus*, occurring north of Cape Hatteras, North Carolina 190
MILLER, ROBERT E., DOUGLAS W. CAMPBELL, and PAMELA J. LUNSFORD. Comparison of sampling devices for the juvenile blue crab, *Callinectes sapidus* ... 196

Notices

NOAA Technical Reports NMFS published during the last 6 mo of 1979 199

☆ GPO 696-404

DEPARTMENT OF COMMERCE
UNITED STATES OF AMERICA

Fishery Bulletin

Marine Biological Laboratory
LIBRARY
DEC 3 1980
Woods Hole, Mass.

Vol. 78, No. 2 April 1980

RANDALL, JOHN E. A survey of ciguatera at Enewetak and Bikini, Marshall Islands, with notes on the systematics and food habits of ciguatoxic fishes 201

SMYTH, PETER O. *Callinectes* (Decapoda: Portunidae) larvae in the Middle Atlantic Bight, 1975-77 251

HUPPERT, D. D. An analysis of the United States demand for fish meal 267

POTTHOFF, THOMAS. Development and structure of fins and fin supports in dolphin fishes *Coryphaena hippurus* and *Coryphaena equiselis* (Coryphaenidae) 277

KNIGHT, MARGARET D. Larval development of *Euphausia eximia* (Crustacea: Euphausiacea) with notes on its vertical distribution and morphological divergence between populations 313

STONER, ALLAN W. Feeding ecology of *Lagodon rhomboides* (Pisces: Sparidae): variation and functional responses 337

MEAD, JAMES G., DANIEL K. ODELL, RANDALL S. WELLS, and MICHAEL D. SCOTT. Observations on a mass stranding of spinner dolphin, *Stenella longirostris*, from the west coast of Florida 353

EBELING, ALFRED W., RALPH J. LARSON, WILLIAM S. ALEVIZON, and RICHARD N. BRAY. Annual variability of reef-fish assemblages in kelp forests off Santa Barbara, California 361

PIETSCH, THEODORE W., and JEFFREY A. SEIGEL. Ceratioid anglerfishes of the Philippine Archipelago, with descriptions of five new species 379

RICHARDSON, SALLY L., JEAN R. DUNN, and NANCY ANNE NAPLIN. Eggs and larvae of butter sole, *Isopsetta isolepis* (Pleuronectidae), off Oregon and Washington 401

WEINSTEIN, MICHAEL P., SIDNEY L. WEISS, RONALD G. HODSON, and LAWRENCE R. GERRY. Retention of three taxa of postlarval fishes in an intensively flushed tidal estuary, Cape Fear River, North Carolina 419

OLIVER, JOHN S., PETER N. SLATTERY, LARRY W. HULBERG, and JAMES W. NYBAKKEN. Relationships between wave disturbance and zonation of benthic invertebrate communities along a subtidal high-energy beach in Monterey Bay, California 437

FERRARO, STEVEN P. Daily time of spawning of 12 fishes in the Peconic Bays, New York 455

BULLARD, FERN A., and JEFF COLLINS. An improved method to analyze trimethylamine in fish and the interference of ammonia and dimethylamine 465

(Continued on back cover)

U.S. DEPARTMENT OF COMMERCE

Philip M. Klutznick, *Secretary*

NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION

Richard A. Frank, *Administrator*
Terry L. Leitzell, *Assistant Administrator for Fisheries*

NATIONAL MARINE FISHERIES SERVICE

Fishery Bulletin

The *Fishery Bulletin* carries original research reports and technical notes on investigations in fishery science, engineering, and economics. The Bulletin of the United States Fish Commission was begun in 1881; it became the Bulletin of the Bureau of Fisheries in 1904 and the Fishery Bulletin of the Fish and Wildlife Service in 1941. Separates were issued as documents through volume 46; the last document was No. 1103. Beginning with volume 47 in 1931 and continuing through volume 62 in 1963, each separate appeared as a numbered bulletin. A new system began in 1963 with volume 63 in which papers are bound together in a single issue of the bulletin instead of being issued individually. Beginning with volume 70, number 1, January 1972, the *Fishery Bulletin* became a periodical, issued quarterly. In this form, it is available by subscription from the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402. It is also available free in limited numbers to libraries, research institutions, State and Federal agencies, and in exchange for other scientific publications.

EDITOR

Dr. Jay C. Quast
Scientific Editor, *Fishery Bulletin*
Northwest and Alaska Fisheries Center
Auke Bay Laboratory
National Marine Fisheries Service, NOAA
P.O. Box 155, Auke Bay, AK 99821

Editorial Committee

Dr. Elbert H. Ahlstrom
National Marine Fisheries Service

Dr. Bruce B. Collette
National Marine Fisheries Service

Dr. Edward D. Houde
University of Miami

Dr. Merton C. Ingham
National Marine Fisheries Service

Dr. Reuben Lasker
National Marine Fisheries Service

Dr. Jerome J. Pella
National Marine Fisheries Service

Dr. Sally L. Richardson
Gulf Coast Research Laboratory

Kiyoshi G. Fukano, Managing Editor

The *Fishery Bulletin* (USPS 090-870) is published quarterly by Scientific Publications Office, National Marine Fisheries Service, NOAA, Room 336, 1700 Westlake Avenue North, Seattle, WA 98109. Controlled circulation paid to Finance Department, USPS, Washington, DC 20260.

Although the contents have not been copyrighted and may be reprinted entirely, reference to source is appreciated.

The Secretary of Commerce has determined that the publication of this periodical is necessary in the transaction of the public business required by law of this Department. Use of funds for printing of this periodical has been approved by the Director of the Office of Management and Budget through 31 March 1982.

Fishery Bulletin

CONTENTS

Vol. 78, No. 2 April 1980

RANDALL, JOHN E. A survey of ciguatera at Enewetak and Bikini, Marshall Islands, with notes on the systematics and food habits of ciguatoxic fishes 201
SMYTH, PETER O. *Callinectes* (Decapoda: Portunidae) larvae in the Middle Atlantic Bight, 1975-77 251
HUPPERT, D. D. An analysis of the United States demand for fish meal 267
POTTHOFF, THOMAS. Development and structure of fins and fin supports in dolphin fishes *Coryphaena hippurus* and *Coryphaena equiselis* (Coryphaenidae) 277
KNIGHT, MARGARET D. Larval development of *Euphausia eximia* (Crustacea: Euphausiacea) with notes on its vertical distribution and morphological divergence between populations 313
STONER, ALLAN W. Feeding ecology of *Lagodon rhomboides* (Pisces: Sparidae): variation and functional responses 337
MEAD, JAMES G., DANIEL K. ODELL, RANDALL S. WELLS, and MICHAEL D. SCOTT. Observations on a mass stranding of spinner dolphin, *Stenella longirostris*, from the west coast of Florida 353
EBELING, ALFRED W., RALPH J. LARSON, WILLIAM S. ALEVIZON, and RICHARD N. BRAY. Annual variability of reef-fish assemblages in kelp forests off Santa Barbara, California 361
PIETSCH, THEODORE W., and JEFFREY A. SEIGEL. Ceratioid anglerfishes of the Philippine Archipelago, with descriptions of five new species 379
RICHARDSON, SALLY L., JEAN R. DUNN, and NANCY ANNE NAPLIN. Eggs and larvae of butter sole, *Isopsetta isolepis* (Pleuronectidae), off Oregon and Washington 401
WEINSTEIN, MICHAEL P., SIDNEY L. WEISS, RONALD G. HODSON, and LAWRENCE R. GERRY. Retention of three taxa of postlarval fishes in an intensively flushed tidal estuary, Cape Fear River, North Carolina 419
OLIVER, JOHN S., PETER N. SLATTERY, LARRY W. HULBERG, and JAMES W. NYBAKKEN. Relationships between wave disturbance and zonation of benthic invertebrate communities along a subtidal high-energy beach in Monterey Bay, California 437
FERRARO, STEVEN P. Daily time of spawning of 12 fishes in the Peconic Bays, New York 455
BULLARD, FERN A., and JEFF COLLINS. An improved method to analyze trimethylamine in fish and the interference of ammonia and dimethylamine 465

(Continued on next page)

Seattle, Washington

1980

For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402—Subscription price per year: $12.00 domestic and $15.00 foreign. Cost per single issue: $3.00 domestic and $3.75 foreign.

O'CONNELL, CHARLES P. Percentage of starving northern anchovy, *Engraulis mordax*, larvae in the sea as estimated by histological methods 475
EBEL, WESLEY J. Transportation of chinook salmon, *Oncorhynchus tshawytscha*, and steelhead, *Salmo gairdneri*, smolts in the Columbia River and effects on adult returns 491
BENIRSCHKE, K., MARY L. JOHNSON, and ROLF J. BENIRSCHKE. Is ovulation in dolphins, *Stenella longirostris* and *Stenella attenuata*, always copulation-induced? 507

Notes

PEARCY, WILLIAM G. A large, opening-closing midwater trawl for sampling oceanic nekton, and comparison of catches with an Isaacs-Kidd midwater trawl .. 529
COE, JAMES M., and WARREN E. STUNTZ. Passive behavior by the spotted dolphin, *Stenella attenuata*, in tuna purse seine nets 535
KRAEUTER, JOHN N., and MICHAEL CASTAGNA. Effects of large predators on the field culture of the hard clam, *Mercenaria mercenaria* 538
PARKER, KEITH. A direct method for estimating northern anchovy, *Engraulis mordax*, spawning biomass 541
PITCHER, KENNETH W. Food of the harbor seal, *Phoca vitulina richardsi*, in the Gulf of Alaska 544
JOHNSON, JAMES H. Production and growth of subyearling coho salmon, *Oncorhynchus kisutch*, chinook salmon, *Oncorhynchus tshawytscha*, and steelhead, *Salmo gairdneri*, in Orwell Brook, tributary of Salmon River, New York 549

Vol. 78, No. 1 was published on 28 August 1980.

The National Marine Fisheries Service (NMFS) does not approve, recommend or endorse any proprietary product or proprietary material mentioned in this publication. No reference shall be made to NMFS, or to this publication furnished by NMFS, in any advertising or sales promotion which would indicate or imply that NMFS approves, recommends or endorses any proprietary product or proprietary material mentioned herein, or which has as its purpose an intent to cause directly or indirectly the advertised product to be used or purchased because of this NMFS publication.

A SURVEY OF CIGUATERA AT ENEWETAK AND BIKINI, MARSHALL ISLANDS, WITH NOTES ON THE SYSTEMATICS AND FOOD HABITS OF CIGUATOXIC FISHES[1]

JOHN E. RANDALL[2]

ABSTRACT

A total of 551 specimens of 48 species of potentially ciguatoxic fishes from Enewetak and 256 specimens of 23 species from Bikini, Marshall Islands, were tested for ciguatoxin by feeding liver or liver and viscera from these fishes to mongooses at 10% body weight (except for sharks, when only muscle tissue was used.) The fishes are representatives of the following families: Orectolobidae, Carcharhinidae, Dasyatidae, Muraenidae, Holocentridae, Sphyraenidae, Mugilidae, Serranidae, Lutjanidae, Lethrinidae, Carangidae, Scombridae, Labridae, Scaridae, Acanthuridae, and Balistidae. The species selected were all ones for which toxicity can be expected, including the worst offenders from reports of ciguatera throughout Oceania; only moderate to large-sized adults were tested. In all, 37.3% of the fishes from Enewetak and 19.7% from Bikini gave a positive reaction for ciguatoxin. Because liver and other viscera are more toxic than muscle, the percentage of positive reactions at the level which might cause illness in humans eating only the flesh of these fishes collectively would drop to 16.2 for Enewetak and 1.4 for Bikini. This level of toxicity is not regarded as high for Pacific islands, in general.

Because ciguatoxin is acquired through feeding, the food habits of these fishes were investigated. Most of the highly toxic species, including seven of the eight causing severe illness or death in the test animals (*Lycodontis javanicus*, *Cephalopholis argus*, *Epinephelus hoedtii*, *E. microdon*, *Plectropomus leopardus*, *Aprion virescens*, and *Lutjanus bohar*) are primarily piscivorous. Some such as *Lethrinus kallopterus* (which also produced a mongoose death) feed mainly on echinoids and mollusks. Among the larger herbivorous fishes that were tested, only one individual of *Kyphosus* and two of *Scarus* caused a weak reaction in the test animals.

In view of the importance of correct identification of the ciguatoxic fishes, diagnostic remarks and an illustration are provided for each of the species tested. Some alteration in scientific names was necessary for a few of the fishes.

The Marshall Islands are the easternmost islands of Micronesia and of the Trust Territory of the Pacific Islands. They consist of 34 low islands, most of which are atolls, and numerous reefs which occur between lat. 4°30′ and 15°N and long. 161° and 173° E. They lie in two parallel groups in a northeast-southwest direction, the easternmost being the Ratak ("Sunrise") Chain and the westernmost the Ralik ("Sunset") Chain.

Two types of fish poisoning are known from the Marshall Islands: tetraodontid (puffer) poisoning (Hiyama 1943; Yudkin 1944; Halstead 1967) and ciguatera. This paper is restricted to the latter toxemia. It results from the ingestion of a great variety of tropical reef and semipelagic fishes. Ciguatoxin is thermostable, hence unaffected by cooking or freezing of the fishes. It is not the result of decomposition but is present to a varying degree in the different tissues of fishes when entirely fresh. The severity of the illness and the symptomatology depend upon the concentration of the toxin and the amount of fish eaten; fatalities are rare. Symptoms appear about 1-10 h after a toxic fish is consumed; those most commonly given are: weakness or prostration; diarrhea; tingling or numbness of the lips, hands, and feet; confusion of the sensations heat and cold; nausea; joint and muscular pain; inability to coordinate voluntary muscular movements; difficulty in breathing; burning urination; and itching. Probably the most common diagnostic symptoms are unpleasant tingling sensations of the palms of the hands and soles of the feet on contact with cool materials and the feeling of heat when cold objects are touched or cold liquids taken into the mouth. Light cases may not exhibit these sensations, however.

The Marshall Islands have long been known to harbor ciguatoxic fishes. The earliest report from these islands seems to be that of Steinbach (1895) who wrote of fishes being toxic on the west side of

[1]Contribution of the Mid-Pacific Research Laboratory.

[2]Bernice P. Bishop Museum, Box 19000-A, Honolulu, HI 96819.

Manuscript accepted October 1979.
FISHERY BULLETIN: VOL. 78, NO. 2, 1980.

the lagoon at Jaluit. Becke (1901) recorded poisonous fishes from Ralik (Ebon), the southernmost atoll in the Marshalls (reference from Halstead 1967). With the takeover of the Marshalls by Japan at the start of World War I (1914), the documentation of ciguatera at these islands shifted to the Japanese. Hishikari (1921), Matsuo (1934), and Hiyama (1943) published on poisonous fishes at Jaluit. Some fishes in the vicinity of Utirik Island, Utirik Atoll, have been reported as poisonous (Hydrographic Office, U.S. Navy 1945).

Historically, Jaluit was the principal atoll of the Marshalls. It was the center of government, had the greatest shipping activity, and the highest population (1,683 in 1933). As a result of military activity during World War II, Kwajalein (the largest atoll in the world) and Majuro became more important. Majuro is the District Administrative Center of the islands. By 1958 the population was 3,336 (compared with 783 in 1935), whereas the population at Jaluit had declined to 1,112 in 1958 (Robson 1959).

Concurrent with the buildup in population and commerce at Majuro and Kwajalein was the appearance of ciguatera (or at least the first records in the literature of its incidence). Halstead and Lively (1954) reported one death and five persons seriously ill from the consumption of a moray eel at Kwajalein. Bartsch et al. (1959, table 2) documented the marked increase in cases of fish poisoning at the hospital at Majuro; there were 22 in 1955 (all in the last half of the year), 100 in 1956, and 211 in 1957. Banner and Helfrich (1964) stated that the atolls in the Marshall Islands where poisonous fishes are most commonly found are Kwajalein, Mille, Ailinglaplap, Jaluit, and Majuro. They tested numerous fishes of many species from Enewetak (formerly spelled Eniwetok) collected in 1958, but none were found to be toxic. Balaz,[3] on the other hand, interviewed Chief Johannes, the last remaining traditional chief of the Enewetak people, at Majuro on 15 March 1974. Johannes stated that poisonous fishes were known at the atoll at the time of his departure in 1946 from the islands of the eastern side between the deep passage and the northern end. It should be pointed out, however, that a short-term field survey of ciguatera at an atoll, such as that carried out by Banner and Helfrich, is difficult to equate to the continuous human bioassay of a population of native people dependent on fishes as their principal source of protein. One should also emphasize that even in highly toxic sectors, the percentage of poisonous fishes that will cause ciguatera when eaten is small. Nevertheless, only a few cases in an area may be needed to prevent residents from fishing in that area.

The atolls of Enewetak and Bikini are located at the northern end of the Ratak Chain 165 mi apart between lat. 11° and 12° N. The native people of Bikini were moved from their island to Rongerik Atoll and later to Kili Island when a series of nuclear explosion tests were carried out by the United States beginning in 1946. The people of Enewetak were transferrred to Ujelang Atoll in 1947 for the same reason. When repatriation of these Micronesian people was contemplated, a question arose as to the current level of toxicity of the food fishes of Bikini and Enewetak.

Fluctuation in the toxicity of fishes in reef ecosystems has long been recognized (Banner and Helfrich 1964; Cooper 1964; Halstead 1967; and Helfrich and Banner 1968). Furthermore, Randall (1958) hypothesized that disruptions of the marine environment resulting in the creation of new surfaces (particularly the repetitive formation of new surfaces) in potentially ciguatoxic areas may be linked to outbreaks of the toxemia. This hypothesis has received support from Cooper (1964) who related toxic sectors in the Gilbert Islands to the locations of wrecks and anchorages, by Helfrich et al. (1968) who documented the first outbreak of ciguatera at Washington Island, Line Islands, following the wreck of the MS *Southbank* in late 1964, and by Bagnis (1969) who reported numerous cases of ciguatera at the previously nontoxic atoll of Hao in the Tuamotu Archipelago after the atoll was altered as a staging area for nuclear testing at Mururoa.

de Sylva (1963) misinterpreted this hypothesis. He stated that Randall found poisonous fishes in estuarine areas. On the contrary, Randall reported toxic fishes in the Society Islands from certain areas of slight or intermittent freshwater drainage which are ordinarily flushed with clear water from the open sea. During periods of heavy rain the freshwater runoff to a normally marine habitat may cause death of stenohaline sessile marine animals, thus forming a new surface for benthic growth.

After stating that the basic toxic organism must be benthic, Randall (1958) wrote, "Since obligately herbivorous fishes and detritus-feeding

[3]George H. Balaz, Research Associate, Hawaii Institute of Marine Biology, pers. commun. 1974.

fishes may be poisonous, the toxic organism would most likely be an alga, a fungus, a protozoan, or a bacterium." He added that if it were an alga it must be fine because certain potentially toxic surgeonfishes are unable to feed on coarse types. Of the algae, he wrote that blue-greens were the most probable source of ciguatoxin.

Yasumoto et al. (1977), however, have shown that the "likely culprit" of ciguatera is a dinoflagellate which lives attached to dead coral or benthic algae. Though identified initially as a new species of *Diplopsalis*, it was later shown (Taylor 1979) to be a new genus as well. Subsequently, Adachi and Fukuyo (1979) named it *Gambierdiscus toxicus*. Although a fat-soluble toxin, later identified as ciguatoxin, was isolated from wild dinoflagellates of this species, this organism produced "... only meager amounts of ciguatoxin, if any,..." under culture conditions (Yasumoto et al. 1979).

The author first visited Enewetak in 1967, then in use as the terminus of a missile range by the United States. The resident personnel had been informed of the hazard of ciguatera, and local reef fishes were not served in the mess. In spite of the warning, some cases of ciguatera still occur, especially with the crews on supply ships to the island who sometimes catch and eat fishes, particularly red snapper, *Lutjanus bohar*, from the vessels before they could be informed of the danger. The most recent case was reported by Roth.[4]

In 1968 six residents of the atoll ate a large reddish brown grouper with small blue spots (probably *Plectropomus leopardus*) that one of them had caught off the garbage pier at the southwest end of Enewetak Island. They had asked a cook in the mess hall to prepare the fish for a meal. The cook refused, explaining that the species was one which could make them sick. Disbelieving, the men took the fish to their quarters and cooked it themselves. They all contracted ciguatera and were hospitalized (Spillman).[5]

These cases of fish poisoning and the knowledge that the marine environments of both Enewetak and Bikini have indeed been disrupted underlined the need for a survey of ciguatera at the two atolls.

The survey was supported by the U.S. Energy Research and Development Administration (now Department of Energy). The field work at Enewetak was based at the Mid-Pacific Marine Laboratory, and the fishing at Bikini was carried out from the RV *Liktañur*.[6] The testing of fishes for ciguatoxin was done at the Hawaii Institute of Marine Biology, University of Hawaii, under the supervision of A. H. Banner.

Six fishing expeditions of 2 to 4 wk duration were dispatched from Hawaii to Enewetak within the period September 1974-May 1978. There were four fishing cruises to Bikini (fishing periods of 3-7 days at the atoll) from December 1974 to July 1976. In addition, 12 potentially toxic *L. bohar* were caught from the *Liktañur* at the atoll of Rongelap in November 1975.

Fishes were collected by spearing, hook and line, trolling lures, explosives, and the ichthyocide rotenone. The specimens were held in chests of crushed ice until they were returned either to the Mid-Pacific Marine Laboratory or the *Liktañur*. They were then measured and weighed, tagged with a metal tag, and a sample taken for testing which included the liver, other viscera, and muscle. A data sheet was filled out for each specimen; the upper half of each sheet was used for field data and the lower half to record the testing for toxicity. A chart of the atoll was printed on the back of each data sheet (separate sets of sheets were maintained for Enewetak and Bikini) so that the locality of capture could be recorded. At Enewetak the entire fish was frozen after the sample was taken for testing. Aboard the *Liktañur* only the samples were retained. The Enewetak specimens, which proved to be highly toxic (rated 4 or 5, see below), were transported frozen to the University of Hawaii for use in biochemical and pharmacological research on ciguatoxin; the remaining fishes were either discarded or used as bait or chum.

For the testing, the samples of fish were fed to mongooses (*Herpestes mungo*) in single meals at 10% body weight. The mongoose is a good animal for the bioassay of ciguatoxin (Banner et al. 1960) because it has a symptomology similar to humans suffering from ciguatera, it retains a meal of toxic fishes (in contrast to cats which are prone to regurgitate fish when it is very poisonous), and because of its availability in Hawaii (where it is regarded as a pest). The mongoose symptoms were

[4]Robert M. Roth, Capt. USAF, MC., Command Surgeon, Joint Task Group, Enewetak, described the illness (symptoms typical of ciguatera) of Francisco Romolor, age 28, a civilian deckhand on the cargo ship *Muskingum*, following ingestion of a red snapper caught in the lagoon (pers. commun. 2 June 1978).

[5]Louis C. Spillman, Jr., Chief Medical Officer, Enewetak, pers. commun. 1968.

[6]The RV *Liktañur* is a converted U.S. Navy LCM, 115 ft in length, operated then by the U.S. Energy Research and Development Administration as a research and supply vessel.

divided into five progressive categories from 1 (diarrhea, slight weakness, and flexion of the forelimbs) to 5 (death within 48 h). The lack of symptoms was recorded as 0. The tests which resulted in a reaction of 4 or 5 were repeated on other mongooses if sufficient material was available. Also any questionable or unexpected tests were repeated.

Two tests were run on most of the fishes, one based on the feeding of liver or liver and viscera to the mongooses and one on muscle tissue. The liver of a toxic fish invariably gave a stronger reaction than muscle. A reaction of 3 to liver feeding would generally elicit a reaction of 1 with flesh. Helfrich et al. (1968) found liver more than 50 times as toxic as the muscle tissue of *L. bohar*. The remaining viscera are also more toxic than somatic muscle. Since the liver alone was often insufficient in mass to provide a meal to a mongoose at 10% body weight, it was usually necessary to combine it with other viscera (generally alimentary tract tissue).

The level of toxicity reported herein is from the liver-viscera feeding, with the exception of sharks. Shark liver may cause a toxemia from the high level of vitamin A. Furthermore, it was noted that mongooses will either not eat shark liver or will not consume enough to equal 10% of their body weight. Thus the toxicity data on sharks are based on muscle tissue alone.

Once a mongoose exhibited symptoms of ciguatera, it was not used again for testing. If it showed no symptoms at all, it was used a second time, but only after a period of at least 1 wk had elapsed. No mongooses were fed potentially toxic fish more than three times even when no symptoms were elicited. The reason for this is the known tendency for ciguatoxin to accumulate in a test animal. Though a fish may cause no illness when eaten, it may still have some toxin at the subsymptomatic level. Eating several such fishes in succession might result in a positive test for the last one, even though there was insufficient toxin to produce illness in a mongoose consuming such a fish for the first time.

The results of our first sampling of potentially toxic fishes at Enewetak and Bikini did not indicate a high level of toxicity. Only the larger individuals of the usual offending species were poisonous. Most of these species are carnivores, in particular those feeding heavily on fishes (Randall 1958). Therefore, subsequent fishing was concentrated on the larger fishes of these species. Because of this selectivity, both for species and size, more fishing effort was spent per fish caught; however, this meant less effort expended later in useless testing.

Prior to the present study, information on the food habits of ciguatoxic fishes was insufficient for most species. When a trained marine biologist familiar with the Marshallese marine biota was present, an analysis was made of the stomach contents of the fishes that were caught. Since ciguatoxin is known to pass through food chains to the larger fishes, where it is concentrated, analyses of the stomach contents of these fishes are needed for an understanding of the feeding interrelationships.

Some previously unpublished stomach-content

TABLE 1.—Summary of mongoose feeding tests (liver-viscera, sharks excepted) of fishes collected at Enewetak (0 = nontoxic; 5 = death of test animal).

Species	Intensity of reaction					
	0	1	2	3	4	5
Nebrius ferrugineus	2					
Carcharhinus albimarginatus	4					
C. amblyrhynchos	11		1			
C. galapagensis	1					
C. limbatus			1			
Galeocerdo cuvier	2					
Triaenodon obesus	8					
Taeniura melanospilos	1					
Lycodontis javanicus			2	1	3	3
Adioryx spinifer	6					
Sphyraena barracuda	3	1	2	1		
Cephalophalis argus	2	3	3		1	
Epinephelus fuscoguttatus	2		4	1		
E. hoedtii	6	3	1		1	
E. maculatus	8	3				
E. microdon	8	3	8	13	5	2
E. socialis	2					
E. tauvina	4	1	1			
Plectropomus leopardus	12	6	8	4		1
P. melanoleucus			1			
P. truncatus			1			
Variola louti	13	4		2		
Aprion virescens	8	1		1	1	
Lutjanus bohar	56	22	11	5		1
L. fulvus	2					
L. gibbus	21	5	2	3		
L. monostigmus	1	1	1			
Macolor niger	23	2				
Lethrinus amboinensis	24					
L. kallopterus	14	2	2			1
L. miniatus	6			3		
L. xanthochilus	2					
Monotaxis grandoculis	4	1				
Kyphosus cinerascens	1	1				
Caranx ignobilis	3	2				
C. lugubris	11	2	1	1		
C. melampygus	24	4	1	1		
C. sexfasciatus	2					
Gymnosarda unicolor	7	4	1	1		
Cheilinus undulatus	6		1			
Coris aygula	4	1				
Epibulus insidiator	5					
Hipposcarus harid	3	1				
Scarus gibbus	18	1				
S. rubroviolaceus	3					
Acanthurus xanthopterus	2					
Balistoides viridescens	1					
Totals	346	74	53	37	11	8

analyses obtained by the author from localities other than the Marshall Islands have been included in this report. The food habit data are presented in the species accounts following the assay of toxicity.

The length measurement most often used for bony fishes was standard length (SL). This was taken from the front of the snout to the end of the hypural plate (hence base of caudal fin). When the method of measuring length is not specified, standard length is intended. Fork length (FL) was used for carangids and scombrids because scutes or keels laterally on the caudal peduncle prevent the accurate external determination of the base of the caudal fin. Total length (TL) was employed for eels, nurse sharks, and some proportional measurements. The length usually given for requiem sharks is precaudal length (PCL).

Schultz and collaborators (1953-66) was the primary reference for the identification of ciguatoxic fishes and the fishes from their stomachs. Enewetak and Bikini were among the islands from which large collections of fishes were made for this systematic work. When names other than those given by Schultz and collaborators are used, an explantion is given in the species accounts.

The species of ciguatoxic fishes which were studied are discussed in approximate phylogenetic sequence below. The results of the mongoose feeding tests are summarized in Table 1 for Enewetak and Table 2 for Bikini.

TABLE 2.—Summary of mongoose feeding tests (liver-viscera, sharks excepted) of fishes collected at Bikini (0 = nontoxic; 5 = death of test animal).

Species	Intensity of reaction					
	0	1	2	3	4	5
Carcharhinus amblyrhynchos	1					
Galeocerdo cuvier	1					
Sphyraena barracuda	1	1	1			
S. forsteri			2			
Crenimugil crenilabis	3					
Epinephelus hoedtii	1					
E. maculatus	2					
E. microdon	2	1	4	1		1
E. tauvina	1		1			
Plectropomus leopardus	1					
Variola louti	2					
Aprion virescens	7	1				
Lutjanus bohar	112	15	8	6	2	
L. gibbus	32	3				
L. monostigmus	4	1				
Lethrinus amboinensis	9					
L. kallopterus	2					
L. miniatus	12					
L. xanthochilus	2					
Caranx ignobilis	2					
C. melampygus	6					
Gymnosarda unicolor	3					
Pseudobalistes flavimarginatus	2					
Totals	208	22	16	7	2	1

RESULTS

Orectolobidae (Nurse Sharks)

Nebrius ferrugineus (Lesson) (Figure 1): Like other orectolobids, this shark has a prominent nasal barbel, relatively small mouth, the fourth and fifth gill openings over the pectoral base, and the two dorsal fins set posteriorly on the body. The teeth, which are small and in numerous rows (the first three or four functional), have a large central cusp with four to six smaller cusps on each side (the teeth of the related genus *Ginglymostoma* have an even larger central cusp and only two small cusps on each side). The two dorsal fins are of nearly equal size, the first originating slightly anterior to the origin of the pelvic fins and the second distinctly anterior to the origin of the anal fin; the caudal fin is about 30% TL.

Nebrius concolor Rüppell appears to be a junior synonym. Bass et al. (1975b) employed this name,

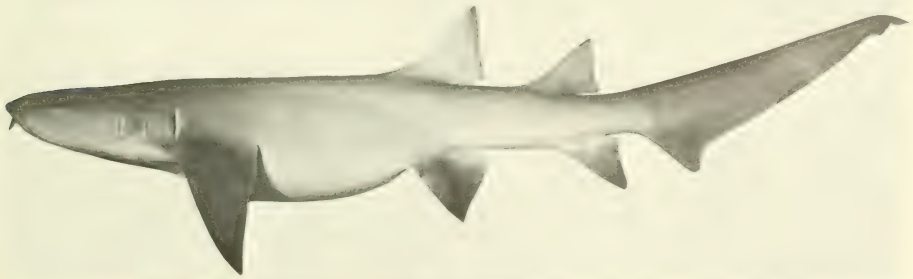


FIGURE 1.—*Nebrius ferrugineus*, 1,080 mm PCL, 1,496 mm TL, 18.1 kg, Enewetak, Marshall Islands.

but admitted that Lesson's *ferrugineus* might have priority.

This shark is a shallow-water species, usually seen at rest on the bottom during daylight hours. It is not common in the Marshall Islands. Two specimens were obtained from Enewetak, 1,400 and 1,487 mm TL, weighing 11.7 and 14.1 kg. The flesh of neither was toxic.

Fourmanoir (1961) stated that the principal food of this shark consists of octopuses and xanthid crabs. Gohar and Mazhar (1964) reported cephalopods, fishes, and parts of corals (*Stylophora*) from the stomachs of Red Sea specimens (the corals were probably accidentally ingested). Hiatt and Strasburg (1960) found a rabbitfish, *Siganus* sp., in the stomach of one of three specimens collected at Enewetak.

The stomach of the smaller of the two specimens taken during the present study contained a surgeonfish, *Acanthurus glaucopareius,* 95 mm SL. Three other Enewetak specimens and one from the Tuamotu Archipelago (to 1,615 mm TL, 20.9 kg) had empty stomachs.

Carcharhinidae (Requiem Sharks)

Carcharhinus albimarginatus (Rüppell) (Figure 2): The silvertip shark is one of three carcharhinid sharks with white on the tips of its fins; the others are the oceanic whitetip shark, *C. maou* (Lesson) (*C. longimanus* a junior synonym), and the whitetip reef shark, *Triaenodon obesus* (Rüppell). The name silvertip has been adopted by Kato et al. (1967) and others to avoid confusion with the other two species with white-tipped fins. The white on the silvertip's fins is not confined to the distal ends but continues along the posterior margins. The apex of the first dorsal fin is somewhat pointed (broadly rounded on *C. maou*); the origin of this fin is over the inner edge of the pectoral fin. The pectorals are about 18% TL (about 28% on *C. maou*). A median interdorsal ridge is present. There are usually 26 upper and 24 lower teeth. The precaudal vertebrae vary from 115 to 125.

Carcharhinus albimarginatus has not been reported as poisonous [Halstead (1967, pl. VI, fig. 3) illustrated it but misidentified the figure as *Triaenodon obesus*], but it would seem to have the potential for causing ciguatera because it preys in part on reef fishes. In the Marshall Islands it was usually seen on exposed outer reefs in water >30 m, though one individual was observed in the Enewetak lagoon in water only 2 m deep. Bass et al. (1973) summarized the depth distribution, noting records to 400 m. This species has attacked man.

The flesh of four silvertips, 933-1,650 mm PCL (15.0-73.5 kg), from Enewetak was nontoxic.

Fourmanoir (1961) reported the following wide variety of fishes from the stomachs of silvertips from Madagascar: *Promethichthys prometheus*, *Pristipomoides typus*, *Seriola songoro*, *Coris gaimard*, *Caesio coerulaureus*, *Acanthocybium solandri*, *Euthynnus pelamis*, and *Neothunnus al-*

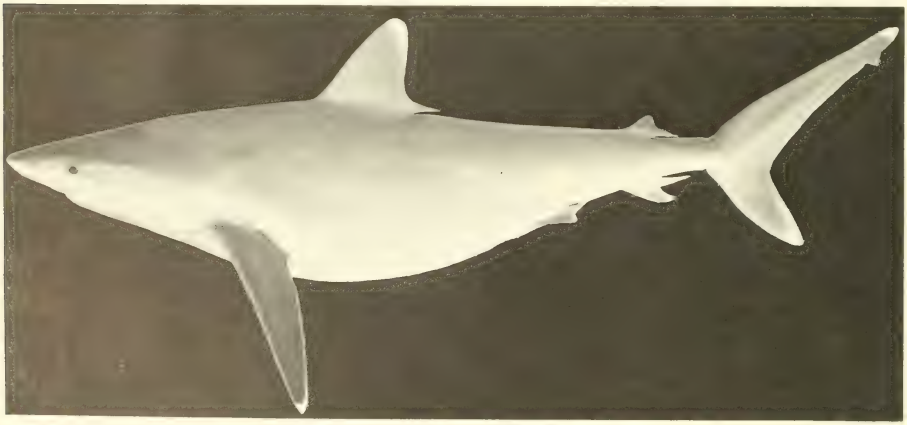


FIGURE 2.—*Carcharhinus albimarginatus*, 1,650 mm PCL, 2,154 mm TL, 73.5 kg, Enewetak, Marshall Islands.

bacora (= *Thunnus albacares*). Bass et al. (1973) examined the stomach contents of 10 specimens of *C. albimarginatus* from the western Indian Ocean. They found teleost fishes (exocoetid, myctophid, several soleids) in seven sharks; a spotted eagle ray, *Aetobatis narinari*, in one; and an octopus in one.

The stomach of one of the Enewetak silvertips (1,240 mm PCL, 1,650 mm TL) contained a gray reef shark, *Carcharhinus amblyrhynchos*, 483 mm PCL and 616 mm TL, as well as the dental plates and pharyngeal mills of three parrotfishes (*Scarus*). The stomachs of the other three sharks were empty.

Carcharhinus amblyrhynchos (Bleeker) Figure 3): This shark, now popularly known as the gray reef shark, was referred to by Schultz in Schultz and collaborators (1953) as *Carcharhinus menisorrah* (Müller and Henle). Bass et al. (1973) and Garrick (in press) are followed in the use of the name *C. amblyrhynchos* herein.

The gray reef shark lacks dark pigment distally on the first dorsal fin, but the tips of the other fins are broadly blackish, and there is a broad black margin posteriorly on the caudal fin. The dark markings on the fins are more evident on live than on dead specimens. The origin of the first dorsal fin is over the pectoral axil or anterior part of the inner edge of the pectoral fin. A short interdorsal ridge is present or absent. There are 26-28 upper teeth and 24-26 lower teeth; the precaudal vertebrae vary from 110 to 117 (two Enewetak specimens had 117).

This shark is abundant in the Marshall Islands. It occurs in many habitats from lagoons to ocean reefs, but it is most commonly encountered in deep channels and outer reef areas. It does not penetrate the shallows as readily as *C. melanopterus*.

The flesh of 11 specimens from Enewetak, 1,017-1,190 mm PCL (17.2-26.3 kg), and 1 from Bikini (3.6 kg, length not taken) was tested. All gave a zero reaction for ciguatoxin. The viscera of one of these, 1,158 mm PCL, from Enewetak produced a reaction of 2, however.

The stomachs of 74 individuals, 520-1,230 mm PCL (2.7-32.4 kg), from Enewetak, Fanning and Palmyra in the Line Islands, Marcus Island, Johnston Island, Palau Islands, and Ducie and Henderson in the Pitcairn Group, were examined for food. Forty-nine stomachs were empty or contained only bait. Three had eaten cephalopods (two octopus, one squid), and the rest contained the remains of fishes (in some cases only the lens of an eye or a few remnants of spines or bones). The fishes that could be identified to family or genus were the following: muraenid, belonid, exocoetid, *Fistularia*, *Decapterus*, *Trachinotus*, *Acanthurus*, and another acanthurid (either *Acanthurus* or *Ctenochaetus*).

In spite of its relatively small size, the gray reef shark constituted a hazard to the personnel of the survey program, particularly when divers were spearfishing or collecting with rotenone. Several

FIGURE 3.—*Carcharhinus amblyrhynchos*, 1,288 mm PCL, 1,640 mm TL, Tahiti, Society Islands.

of these sharks were killed by powerheads when their aggressive behavior and proximity warranted. On 12 July 1975 the companion diver of the author, Russell E. Miller, sustained 7 gashes in his head requiring 25 stitches as the result of an attack by a *C. amblyrhynchos* of about 1,500 mm TL. The shark first exhibited threat posturing (see Johnson and Nelson 1973) at the back of the author. Miller sounded a warning by rapping on his scuba tank with his powerhead handle. The shark immediately turned and swam toward him, repeating the exaggerated sinuous swimming of its threat behavior as it approached. Miller struck the shark with his powerhead but the shell misfired. The shark came on to slash his head (and cut the rubber strap of his face mask) with its upper jaw. On another occasion Gordon W. Tribble had the end of his speargun seized by a gray reef shark and vigorously shaken.

Richard C. Wass (1971) has made a comparative study of the biology of the gray reef shark and the sandbar shark in the Hawaiian Islands.

Carcharhinus galapagensis (Snodgrass and Heller) (Figure 4): This shark is circumtropical in distribution, but as noted by Garrick (1967), it shows a preference for the sea around oceanic islands.

The Galapagos shark has no distinctive markings; it is dark gray dorsally, pale ventrally. The origin of the first dorsal fin is anterior to the inner free corner of the pectoral fin. The second dorsal fin is relatively large for a *Carcharhinus*, its height 2.4-2.8% TL. A distinctive median interdorsal ridge is present on the back. There are 26-30 upper teeth (the anterior upper teeth broadly triangular) and 26-29 lower teeth. The precaudal vertebrae range from 103 to 109.

A single specimen, 1,831 mm PCL, 2,426 mm TL, 41.2 kg, was collected at Enewetak. Its flesh was nontoxic.

Tester[7] examined the stomach contents of 41 Galapagos sharks caught from the Hawaiian Islands; 51% were empty. Sixty percent of the sharks had eaten bony fishes, 35% cephalopods, 20% sharks and rays, and 10% crustaceans. He commented that the larger individuals (maximum length estimated as 10 ft or 3,048 mm) fed mostly on larger fishes which were torn into chunks. He regarded it as a dangerous species; Randall (1963) documented a fatal attack.

Bass et al. (1973) found food in 18 of 22 individuals of this species; 12 of the stomachs contained teleost fishes (serranid, *Platycephalus*, and a flatfish) and 10 had squids or octopuses (plus the shell of a bivalve mollusk).

The Enewetak specimen was empty as were three others 1,460-1,690 mm PCL from the Pitcairn Group. One of 1,580 mm PCL from Rapa contained the head of an unidentified eel.

Carcharhinus limbatus (Valenciennes) (Figure 5): The shark occurs in the Atlantic as well as the Indo-West Pacific. In the Atlantic it bears the common name of blacktip shark, a name which is poor for the species in the Pacific for two reasons.

[7]Tester, A. L. 1969. Final Report, Cooperative Shark Research and Control Program, University of Hawaii. Mimeogr. Rep., 47 + 36 append. p.

FIGURE 4.—*Carcharhinus galapagensis*, 1,831 mm PCL, 2,426 mm TL, 87 kg, Enewetak, Marshall Islands.

FIGURE 5.—*Carcharhinus limbatus*, 1,415 mm PCL, 1,910 mm TL, 38.2 kg, Enewetak, Marshall Islands.

The tips of the fins of Pacific individuals, particularly adults, are only slightly tipped or edged in black. Also the common Indo-West Pacific *C. melanopterus* has very pronounced black tips on its fins (see Randall and Helfman 1973, fig. 1, 2). To avoid confusion in common names, *C. melanopterus* has been referred to by many recent authors as the blacktip reef shark (though Bass et al. 1973, call it the blackfin reef shark).

Carcharhinus limbatus is distinctive in lacking a median ridge on the back between the dorsal fins, having a relatively long snout, and the cusp of its teeth notably narrow and erect. It has 29-32 upper, 28-32 lower teeth, and 88-102 precaudal vertebrae. The color is gray to bronze on the back, white below, with a long band of the dark dorsal color extending posteriorly from the last gill opening into the pale ventral color as far as the pelvic fins.

Two individuals of *C. limbatus* were caught at Enewetak during the ciguatera survey; these constitute the first records of the species from the Marshall Islands. The head of the illustrated specimen (which was 1,415 mm PCL, 1,910 mm TL, and weighed 38 kg) has been preserved in the Bernice P. Bishop Museum under catalog number 18074.

Only the second specimen, which was about 1,700 mm PCL (original data sheet with measurements was lost), was tested for toxicity. The viscera gave a reaction of 2 when fed to a mongoose.

Bass et al. (1973) reported on 55 of 101 sharks of this species with food in their stomachs. Fifty-one of the sharks had eaten teleost fishes, including: *Scomberomorus commerson*, *S. leopardus*, *Pomadasys* sp., *Sarpa salpa*, *Johnius hololepidosus*, *Leiognathus equula*, *Elops saurus*, *Tilapia mossambica*, and a soleid. Six contained elasmobranchs, including a small *C. obscurus* and a *Rhinobatus annulatus*. Two had eaten *Sepia* sp., and one a spiny lobster, *Panulirus homarus*.

The two Enewetak specimens had empty stomachs.

Galeocerdo cuvier (Peron and Lesueur) (Figure 6): The circumtropical tiger shark is readily identified by its broad bluntly rounded snout, distinctive teeth (heavily serrate, convex on the medial margin, and deeply notched on the lateral), low longitudinal keel on the side of the caudal peduncle, and dark bars (though these tend to fade with age).

The flesh of two tiger sharks from Enewetak, 1,770 and 2,410 PCL (72 and 174 kg), and one from Bikini, 1,498 mm PCL, was tested. None of these sharks were toxic. The Bikini specimen was caught at 4:30 a.m. in only 1.7 m of water.

Bigelow and Schroeder (1948) summarized the literature on food habits, danger to man, etc., of this shark. Other authors such as Clark and von Schmidt (1965), Bass et al. (1975a), and Tester (see footnote 7), have added to the list of the great variety of marine animals (mainly fishes) that this species will take as food, as well as sundry items of garbage and refuse discarded into the sea by man.

The stomach of the largest of the Marshall Islands specimens contained the scutes of a green turtle, *Chelonia mydas*, estimated to be 500 mm carapace length and the bait (a gray reef shark).

FIGURE 6.—*Galeocerdo cuvier*, 2,410 mm PCL, 3,055 mm TL, 175 kg, Enewetak, Marshall Islands.

The stomachs of the other two sharks were empty. Three other tiger sharks from Enewetak had food in their stomachs. One of 3,150 mm TL contained shark vertebrae. The second of 3,581 mm TL had the scutes of a green turtle and bird feathers. The third, 3,048 mm TL, was filled with pieces of a porpoise and the digested remains of shark fins.

A tiger shark of 3,327 mm TL from Ua Huka, Marquesas Islands, was empty, as was one of 2,895 mm TL from Oahu. Another from Oahu of 3,048 mm had an extremly distended stomach filled with heads of skipjack tuna (neatly cut by a knife, hence probably discarded from a fishing boat), plastic bags of garbage and aluminum foil, a cat, and two small reef fishes (one a balistid). It also contained the bait (the head of a calf). A 3,100 mm specimem weighing 174.6 kg taken by a set line at night at Rapa had eaten parts of a tiger shark larger than itself (probably from an individual caught on another hook), as well as a seabird.

Triaenodon obesus (Rüppell) (Figure 7): The whitetip reef shark, once classified by most ichthyologists in the family Triakidae, is now recorded as a carcharhinid (Compagno 1973). In spite of its scientific name, it is rather slender compared with most species of the family. Apart from its slim form and white-tipped first dorsal fin and upper caudal lobe, *T. obesus* is distinctive in its very blunt snout and teeth which bear a small cusp on each side of the main central one. It is widespread throughout the tropical and subtropical Indo-West Pacific region and ranges to the eastern Pacific as well. Banner and Helfrich (1964) and Brock et al. (1965) have reported this species as poisonous from Johnston Island.

FIGURE 7.—*Triaenodon obesus*, 1,218 mm PCL, 1,520 mm TL, 23.5 kg, Tahiti, Society Islands.

The toxicity of eight whitetip reef sharks, 1,003-1,183 mm PCL (8.4-22.4 kg), from Enewetak was tested. The flesh of all was negative for ciguatoxin by feeding to mongooses, but the viscera of two gave positive reactions of 1.

Randall (1977) studied the biology of this species. He opened the stomachs of 56 specimens (24 of which were from Enewetak): 33 were empty, 6 had eaten octopuses (2 of these also contained fishes), and the rest had the remains of reef fishes, especially scarids and acanthurids.

Dasyatidae (Sting Rays)

Taeniura melanospilos Bleeker (Figure 8): The specimens collected in the Marshall Islands were initially called *Taeniura brocki* Schultz. However, it now seems more likely that they should be identified as *T. melanospilos* Bleeker. Schultz in Schultz and collaborators (1953) differentiated *T. brocki* by its having the venomous spine inserted "...at about half length of tail..." in contrast to a little behind the first third on *T. melanospilos*, in having the snout contained five times in the greatest width of the disc (given as six by Bleeker for *T. melanospilos*), and in having "...very numerous irregularly shaped small brownish to blackish spots and blotches speckling dorsal surface of disk ...," as opposed to "... numerous rounded black spots ..." for *T. melanospilos*. After noting the measurements of the position of the spine and the length of the tail of his only specimens of *T. brocki*, Schultz wrote, "... end of the tail may have been bitten off...." On the specimen illustrated herein, the spine is inserted at a point 41% the length of the tail from the base. From Schultz' measurements, the snout of *T. brocki* is contained 5.14 times in the width of the disc. The snout of the specimen illustrated herein is contained about 5.3 times in the disc width. Without knowledge of variation of this character and perhaps proportional differences with growth, the differentiation of species on this magnitude of snout length is questionable. Furthermore, Bleeker's (1853) de-

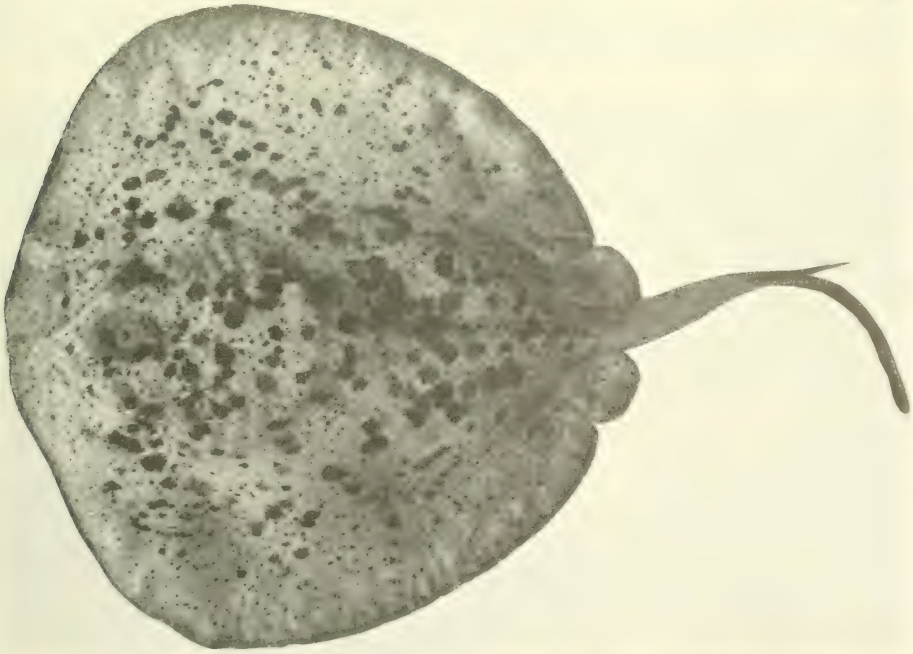


FIGURE 8.—*Taeniura melanospilos*, 1,255 mm disc length, 2,008 mm TL, 69 kg, Enewetak, Marshall Islands.

scription of the dark spots of *T. melanospilos* was not simply round as Schultz stated, but round and oblong and variably small, medium, and large.

One stingray of this species from Enewetak with a disc length of 870 mm (disc width 950 mm; tail length 950 mm), weighing 19.05 kg, was tested. It was not poisonous.

The stomach of this ray was empty. Another of 1,255 mm disc length weighing 68.9 kg collected by the author at Enewetak in 1968 had eaten two labrid fishes (*Xyrichtys*) and a parrotfish, *Scarus* sp. It was a female with seven embryos.

Muraenidae (Morays)

Lycodontis javanicus (Bleeker) (Figure 9): This moray is brown with large dark blotches and numerous small dark spots; the gill opening is in a large black spot; there are no pale margins on the fins. It is probably the species of eel reported by Khlentzos (1950) which poisoned 57 Filipino laborers at Saipan, Mariana Islands. In spite of prompt gastric lavage, 14 of these men became comatose and 2 died.

The severity of illness from the consumption of moray eels led Halstead and Lively (1954) to regard this as a distinct category of fish toxemia which they termed "Gymnothorax poisoning." However, it appears to be principally an acute form of ciguatera, though there is a possibility of involvement of one or more other toxins.

Lycodontis javanicus is not common in the Marshall Islands, but it is abundant (for a large carnivore) at Johnston Island; in recent years it has served as the primary source of ciguatoxin for biochemical and pharmacological study at the University of Hawaii by a team of scientists headed by A. H. Banner.

Nine specimens from Enewetak measuring 1,086-1,540 mm TL and weighing 3.6-13.0 kg were tested. All were toxic, two at the 2 level, one at 3, three at 4, and three at 5 from the feeding of liver and viscera to mongooses. The flesh of two of these eels with a mongoose reaction of 4 was tested; one was a 1 and the other a 2. One of the eels with a mongoose test of 5 for liver-viscera gave a reaction of 3 with flesh.

Brock (1972) studied some aspects of the biology of *L. javanicus*, including an analysis of the toxicity at Johnston Island. Of 1,074 specimens, only 158 (14.7%) contained food; 88.8% of the stomach-content material consisted of fishes (representing 17 different families, the Scaridae predominating). Among the more interesting prey species was

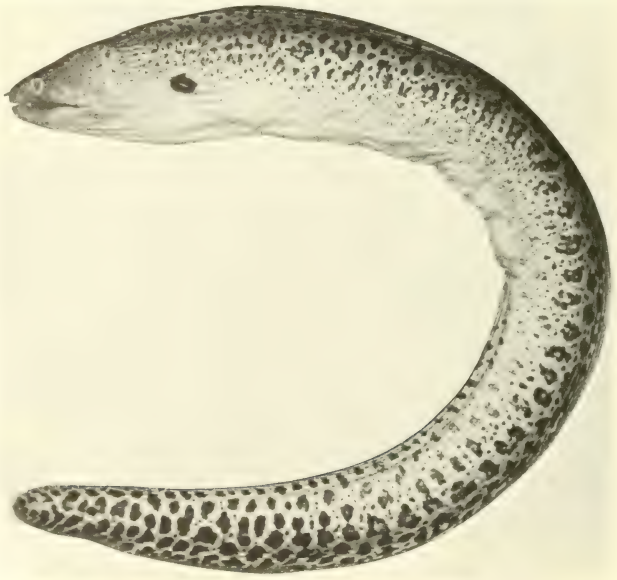


FIGURE 9.—*Lycodontis javanicus*, 732 mm TL, Enewetak, Marshall Islands.

a whitetip reef shark 465 mm PCL, taken from the stomach of a 1,422 mm moray. Octopus and spiny lobster were also eaten.

This is the largest species of moray in the Indo-Pacific region. Schultz (1949) attributed an attack on the late Vernon E. Brock at Johnston Island by a moray of about 10 ft (3,048 mm) in length to be *Enchelynassa canina*. Following a later interview with Brock, Randall (1969) reported that the eel was actually *L. javanicus* and the length 7-8 ft (2,134-2,438 mm). Stephens (1963) noted that the largest moray measured at Johnston during his stay at the island to be 7 ft 10 in (2,388 mm). The author tended to disbelieve occasional reports by divers of individual *L. javanicus* of 10-12 ft (3,048-3,658 mm) until he observed one of an estimated 3,000 mm long off Mafia Island, Tanzania, which was flushed from a cave with rotenone (the eel recovered from the affect of the rotenone and returned to its cave).

The stomach contents of 11 specimens 417-1,905 mm TL (the largest weighed 24.5 kg) were examined during the present study. Six of these eels were from Enewetak, the rest from Oeno, Pitcairn, Johnston, and Truk. Four had empty stomachs. The smallest contained a crab chela. The others had eaten fishes (two contained *Scarus* sp., one *Diodon* sp., and another *Thalassoma purpureum*). The stomach of a 1,540 mm, 13 kg specimen was distended with *Kyphosus cinerascens*, *Acanthurus nigricauda* (identified as *A. nigricans* by Schultz and Woods in Schultz and collaborators 1953, and as *A. gahhm* by Randall 1956), and *A. nigroris*, all of which totalled 1.5 kg. These fishes must be discounted as normal prey, however, as they were undoubtedly eaten as a result of a dynamite station at the Enewetak garbage pier. The eel was collected with a powerhead blast immediately after the dynamite explosion when it was discovered within the area in which many other fishes had just been killed.

Holocentridae (Squirrelfishes)

Adioryx spinifer (Forsskål) (Figure 10): The largest of the squirrelfishes, this species exceeds 300 mm SL. It has a deep body, the depth about 2.5-2.7 in SL, projecting lower jaw, 40-44 lateral line scales, and a well-developed venomous spine at the corner of the preopercle. The color is red and silvery with a deep red spot behind the eye and another on the pectoral axil; the fins are yellow except the spinous dorsal which is deep red. Described from the Red Sea, the species has since

FIGURE 10.—*Adioryx spinifer*, 260 mm SL, Enewetak, Marshall Islands.

been recorded from throughout the tropical Indo-West Pacific. It is often found in caves.

Randall (1958) reported this species as occasionally toxic in Tahiti. In his review of ciguatoxic fishes, Halstead (1967) cited this and three other references.

Six specimens, 232-280 mm SL (0.35-0.66 kg), were collected for assay of toxicity from Enewetak. All were nontoxic.

Randall (1958) found fishes in the stomachs of two adults from Tahiti. Hiatt and Strasburg (1960) examined the stomachs of nine from Enewetak, one of which was empty. Crabs (especially xanthids) dominated the stomach contents of the other specimens: 12% contained stomatopods and 12% fishes. The stomachs of five specimens from Hawaii reported by Hobson (1974) contained crustaceans, mainly caridean shrimps, and xanthid crabs.

For this food-habit study a total of 31 specimens ranging from 182 to 280 mm SL were obtained, principally from Enewetak, but a few from the Red Sea, Society Islands, Hawaiian Islands, and American Samoa. Because this species is nocturnal, like other holocentrids in general, most specimens were collected in early morning hours. Twenty-eight of these fish had food in their stomachs; 82% by volume consisted of crabs, mostly xanthids, 5% fishes (including *Lycodontis rueppelliae* and a prejuvenile acanthurid), and the rest shrimps, a hermit crab, unidentified crustaceans (mostly larval), larval mollusks, and an unidentified worm.

Sphyraenidae (Barracudas)

Sphyraena barracudaa (Walbaum) (Figure 11): The great barracuda is distinctive in having a few blackish blotches on the side, especially posteriorly and ventrally, and the lowest lateral line scale count of the genus (76-85). It is the worst offender for causing ciguatera in the West Indies, due not only to the high level of toxicity of occasional individuals but also to its relative abundance there. The species is far less common in the Indo-West Pacific.

Seven specimens 563-1,182 mm SL (1.5-13.6 kg) from Enewetak were tested, and three from Bikini, 640-1,143 mm SL, the largest 15.0 kg. Three from Enewetak were nontoxic, one was toxic at the level of 1; two gave a reaction of 2; and one (1,050 mm, 12.7 kg) was a 3. The three from Bikini were tested at 0, 1, and 2.

de Sylva (1963) made a study of the systematics and life history of the great barracuda, principally from material from the western Atlantic. He reviewed previous papers which presented limited data on the food habits of this species. Among them was the report by Ommanney in Wheeler and Ommanney (1953) on the fishes found in the stomachs of 5 of 12 specimens of *S. commersoni* (now known to be a junior synonym of *S. barracuda*) from the Seychelles. One of the five contained an unidentified eel and another *Lethrinus ramak*. de Sylva mistakenly reported Ommanney's five barracuda as all having eaten *L. ramak*.

de Sylva opened the stomachs of 901 great barracuda, including juveniles, from various localities in the tropical western Atlantic. Of these, 529 (58.7%) contained food. Fishes were found in 82.2% of the stomachs, plant material in 2.8% (probably accidentally ingested with prey), invertebrates (notably squids and shrimps) in 2.6%, and unidentifiable material in 12.2%. The Hemiramphidae was the most common family of fishes found in the stomachs of 446 adult barracuda from Florida, whereas tetraodontid fishes predominated in the stomach contents of 132 adults from Bimini, Bahamas.

The stomachs of 13 specimens, 560-1,182 mm

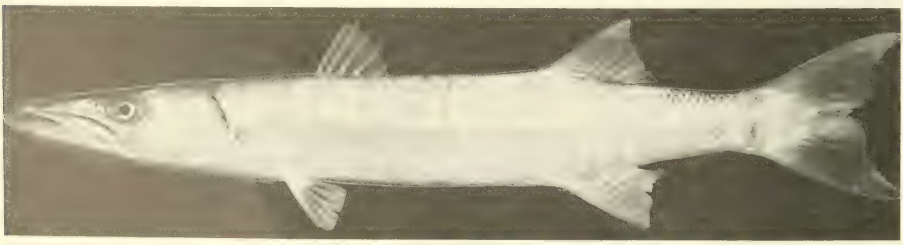


FIGURE 11.—*Sphyraena barracuda*, 524 mm SL, Palmyra, Line Islands.

SL, from the Marshall Islands and Line Islands were examined during the present study. Nine of these fishes had empty stomachs. The rest contained the remains of fishes.

Sphyraena forsteri Cuvier (Figure 12): This barracuda is readily distinguished from all others by its large eye, black blotch in the axil of the pectoral fins, and spiniferous plates on its first gill arch instead of gill rakers or no trace of rakers at all.

de Sylva (1973:18) wrote that this species of barracuda has been implicated in poisoning but added that the examples appear to be misidentifications of *S. barracuda*. Hiyama (1943, pl. 3, fig. 9), however, did not confuse his specimens with *S. barracuda*. He reported *S. forsteri* from the Marshall Islands as slightly poisonous from feeding flesh to cats and mice.

Only two individuals of this species were caught during the survey, both from Bikini and both the same size (610 mm SL, 1.8 kg). Each produced a toxic reaction of 2.

The stomach of one of these fish contained fish remains; the other was empty.

Mugilidae (Mullets)

Crenimugil crenilabis (Forsskål) (Figure 13): This large mullet has a deeply emarginate caudal fin, a black spot at upper pectoral base, and 37-39 rows of scales between the gill opening and the caudal base. Widespread in the tropical Indo-West Pacific region, it is usually seen in small aggregations in the shallows of lagoons and on outer reef flats. It appears to feed on fine algae and detritus from the substratum. After feeding on a sandy bottom it has been observed to expel sand from its gill openings. The spawning by a large school at the surface at night in the Enewetak lagoon was described by Helfrich and Allen (1975). *Crenimugil crenilabis* has been reported as poisonous by Randall (1958) from the Society Islands. It is probably the species of mullet that Ross (1947)

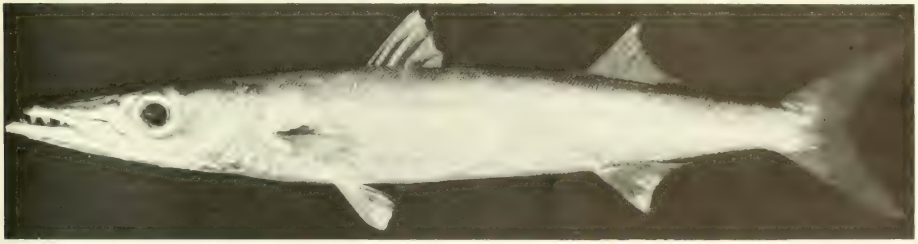


FIGURE 12.—*Sphyraena forsteri*, 540 mm SL, 1.2 kg, Enewetak, Marshall Islands.

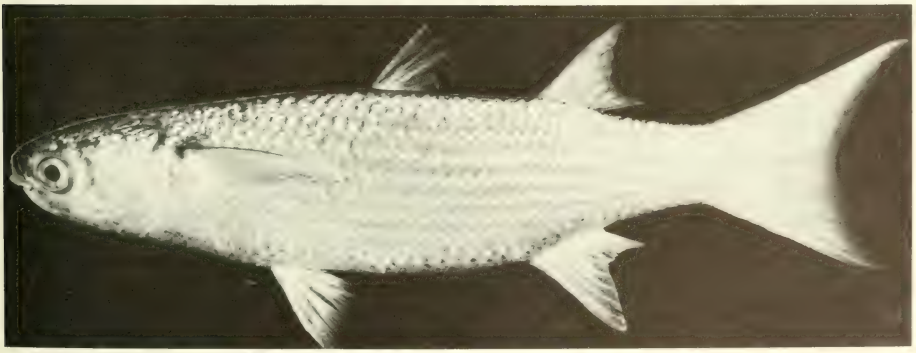


FIGURE 13.—*Crenimugil crenilabis*, 337 mm SL, Enewetak, Marshall Islands.

found toxic at Fanning, Line Islands (Randall 1958).

Three specimens, 248-406 mm (0.4-0.7 kg), were obtained for testing from Bikini. None were toxic.

Serranidae (Groupers)

Cephalopholis argus Bloch and Schneider (Figure 14): This common brown blue-spotted grouper has 9 dorsal spines (in contrast to 11 for the groupers of the genus *Epinephelus*). It does not reach large size, but is has occasionally been implicated in ciguatera. Although it is most abundant in outer reef areas, it also occurs on lagoon reefs.

A total of nine specimens from Enewetak were tested; these ranged from 278 to 390 SL (0.45-1.6 kg). Two were nontoxic, three gave a reaction of 1, three were recorded as 2, and the largest was a 4.

Randall (1955a) found 8 of 10 individuals of this grouper from the Gilbert Islands with empty stomachs; 1 had eaten a fish (probably from rotenone), and 1 a penaeid shrimp. Randall and Brock (1960) obtained 280 specimens for food-habit study, of which 182 were empty; 77.5% contained fishes and the rest crustaceans. Hiatt and Strasburg (1960) reported on food in five of eight stomachs from the Marshall Islands as crustaceans, fishes, and polychaetes. Helfrich et al. (1968) examined the stomachs of 51 from Palmyra; they found fishes in 89% of the stomachs and crustaceans. Harmelin-Vivien and Bouchon (1976) caught 43 *C. argus* for stomach-content analyses in Madagascar. They found fishes 95.7% by weight, shrimps 3.9%, and stomatopods 0.4% in the stomachs.

For the present study the stomachs of 39 specimens, 145-392 mm SL, from Enewetak, Society Islands, Samoa Islands, Palmyra, Marcus Island, and Pitcairn, were examined. Twenty-six were empty, one had eaten a stomatopod, and the rest contained fishes (two of these were the acronurus stage of Acanthuridae, one a labrid, one an antennariid, and one *Apogon kallopterus*).

Epinephelus fuscoguttatus (Forsskål) (Figure 15): The name *E. fuscoguttatus* was used by Schultz in Schultz and collaborators (1953) for the more common related species properly called *E. microdon* (Bleeker) (systematic clarification by Randall 1964). The two are similar in morphology and color. *Epinephelus fuscoguttatus* has higher pectoral ray counts (18 or 19, compared with 16 or 17 for *E. microdon*) and more lower limb gill rakers (18-21, including rudiments, compared with 16 or 17 for *E. microdon*).

This grouper is a large species; it is not common. Furthermore, it is the most wary of Marshall Islands groupers. Seven specimens (335-780 mm SL, 3.1-15.4 kg) were taken at Enewetak for testing, and none at Bikini. Four of the seven were toxic at the 2 level, and one (710 mm SL) was a 3.

Harmelin-Vivien and Bouchon (1976) caught four individuals of this species for food-habit study in Madagascar. The stomachs contained 94.2% fishes by weight and 5.8% brachyuran crabs.

The stomachs of seven specimens from

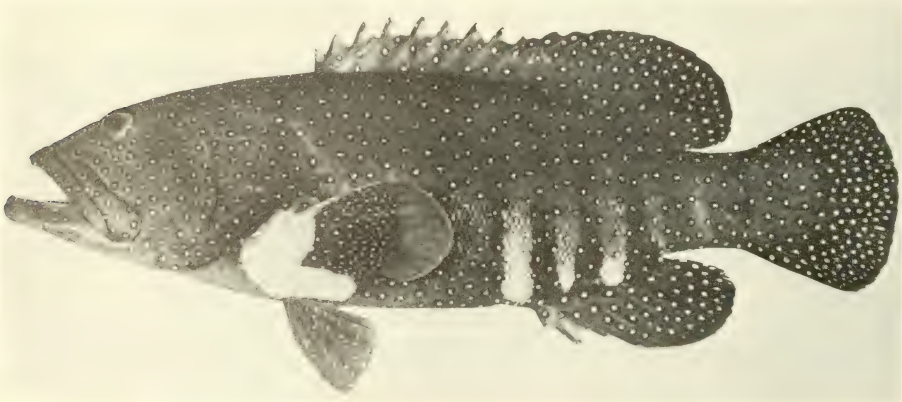


FIGURE 14.—*Cephalopholis argus*, 232 mm SL, Tahiti, Society Islands.

FIGURE 15.—*Epinephelus fuscoguttatus*, 551 mm SL, 5.9 kg, Gulf of Aqaba, Red Sea.

Enewetak were examined. Four were empty, one had an octopus, one had fish remains, and the last contained unidentified tissue which appeared to be cephalopod in origin. A specimen 408 mm SL from the Red Sea had crab remains in its stomach.

Epinephelus hoedtii (Bleeker) (Figure 16): Schultz in Schultz and collaborators (1953) described this fish as new from the Marshall Islands, naming it *E. kohleri*. It is relatively deep bodied and has a slightly emarginate to truncate caudal fin. He differentiated it from "... all of the 'varieties' of *flavocaeruleus* described by Boulenger in having the body spotted with dark blotches in addition to tiny dark specks." Although more study is needed of the complex of forms which Boulenger

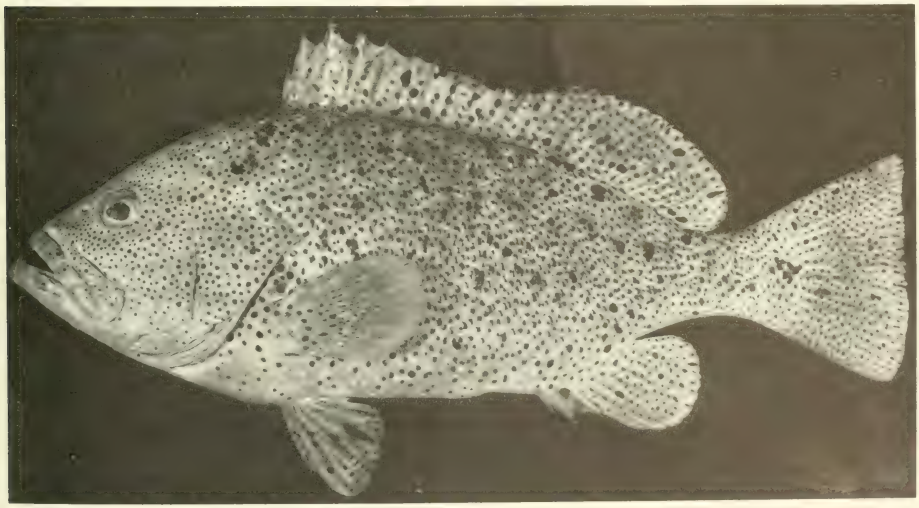


FIGURE 16.—*Epinephelus hoedtii*, 319 mm SL, Enewetak, Marshall Islands.

(1895) regarded as varieties of *flavocaeruleus*, I believe that the variety called *E. hoedtii* (Bleeker) is a valid species and that Schultz' *E. kohleri* is a junior synonym of it. Adult specimens, such as the type of *E. kohleri*, have the dark blotches, whereas smaller individuals, such as Bleeker's specimens, lack them. Hiyama (1943:81, pl. 18, fig. 49) identified it as *Serranus flavocaeruleus* (Lacepède).

This grouper was found around isolated coral heads in the lagoon of Enewetak. Eleven specimens, 348-429 mm SL, 1.36-2.72 kg, were tested. Six were nontoxic, three gave reactions of 1, one was a 2, and one (400 mm SL) a 4. A single specimen (2 kg) from Bikini was nontoxic.

Hiatt and Strasburg (1960) found fish fragments in the stomach of one of two specimens from the Marshall Islands.

The stomachs of the 11 Enewetak specimens were opened. Five were empty, one (429 mm SL) contained a 520 mm snake eel, *Leiuranus semicinctus*; two had eaten calappid crabs; and the remaining three contained the digested remains of fishes.

Epinephelus maculatus (Bloch) (Figure 17): This dark-spotted grouper was identified as *E. medurensis* (Günther) by Schultz in Schultz and collaborators (1953). It has also been called *E. fario* (Thunberg) by some authors. The oldest valid name, however, is *E. maculatus* (Bloch). Though the author ascertained that the type-specimen is no longer extant, Bloch's description and illustration match that of the juvenile of this species, particularly with reference to the large pale markings. Adults are distinctive in the rather elevated third and fourth dorsal spines; also there are two large dark areas on the dorsal fin and adjacent back which are separated by a pale area (both dark and light areas still have the profusion of small dark spots).

Like *E. hoedtii*, this species is found mainly around coral knolls in sandy stretches of atoll lagoons. Eleven specimens from Enewetak, 270-334 mm SL, 0.45-0.9 kg, were tested. Eight were nontoxic and three gave reactions of 1. Two from Bikini, 343 and 356 mm SL, were nontoxic.

The stomachs of 13 specimens from Enewetak and 2 from Bikini, 270-380 mm SL, were examined. One of 334 mm contained a portunid crab and unidentified fish remains; another of 345 mm had eaten a calappid crab (15% by volume), two microdesmid fish 78 and 86 mm SL (identified as *Gunnellichthys monostigma* by C. E. Dawson), and a digested fish; a third (308 mm SL) also contained *G. monostigma*; a fourth (288 mm SL) an octopus; and two others fish remains. The remaining nine stomachs were empty.

Epinephelus microdon (Bleeker) (Figure 18): This is a common species in the Marshall Islands for a grouper of moderate size. It is found on both

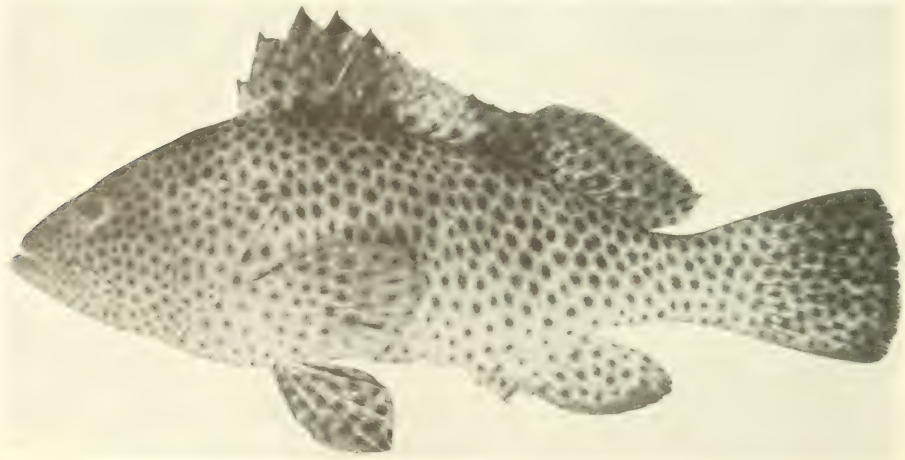


FIGURE 17.—*Epinephelus maculatus*, 280 mm SL, Enewetak, Marshall Islands.

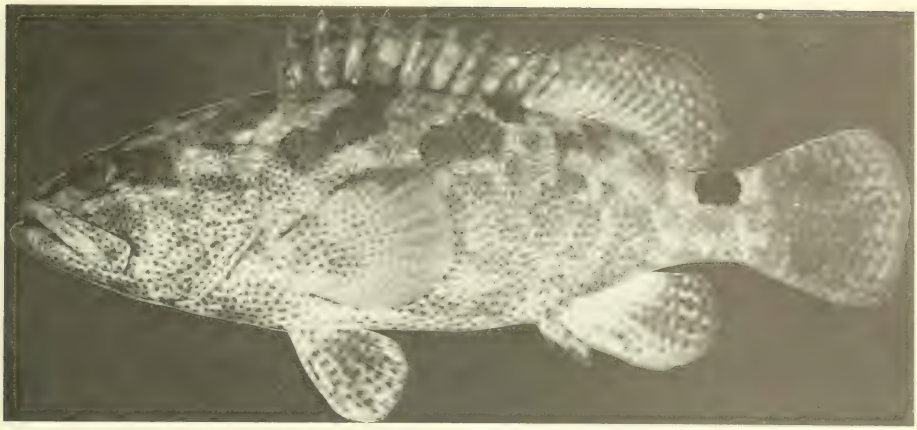


FIGURE 18.—*Epinephelus microdon*, 282 mm SL, Enewetak, Marshall Islands.

ocean and lagoon reefs. As mentioned in the account of *E. fuscoguttatus* above, it has been confused with this species by Schultz and other authors.

Thirty-nine specimens from Enewetak were tested for ciguatera toxin. These ranged from 310 to 470 mm SL and weighed 1.4-3.1 kg. Eight were nontoxic, 3 were toxic at the 1 level, 8 were 2, 13 were 3, 5 were 4, and 2 were 5 (caused death of test animals).

Nine specimens from Bikini, 279-508 mm SL, 0.9-4.1 kg, were tested. Two (279 and 342 mm) were nontoxic, one was poisonous at the 1 level, four were 2, one was 3, and one was 5 (460 mm SL).

Randall and Brock (1960) reported on the food habits of this species (as *E. fuscoguttatus*) from 33 specimens taken in the Society Islands and Tuamotu Archipelago. Of 10 with food in their stomachs, 5 had eaten crustaceans (mainly crabs) and 5 of them fishes. The eight specimens recorded by Hiatt and Strasburg (1960) as *E. fuscoguttatus* were probably *E. microdon*. Three fish had empty stomachs and the remaining five contained fishes and crustaceans.

Helfrich et al. (1968) examined the stomachs of 150 specimens from the Line Islands of which 81 contained food, mainly fishes and crustaceans. The latter accounted for 64% of the total by volume (portunid crabs and scyllarid lobsters were the most frequently recorded). A few of the groupers had eaten gastropods and cephalopods.

For the present food-habit study 44 specimens (210-610 mm SL) were examined, of which 28 were from Enewetak. The remaining 15 were from Palmyra, Tutuila, and Rapa (where the largest specimen was taken). Thirty of the 44 groupers had empty stomachs. Eight contained crabs (mainly porcellanids and portunids; one had eaten the xanthid *Carpilius convexus*), three contained fishes (one identified as *Scarus*), two had eaten octopus, and one a spiny lobster, *Panulirus*.

Epinephelus socialis (Günther) (Figure 19): This grouper has numerous small dark brown spots which tend to coalesce to form irregular longitudinal bands, especially posteriorly. The caudal fin and soft portions of the dorsal and anal fins have narrow pale margins and broad blackish submarginal zones. It is found mainly on the outer reef flat of the atoll environment, sometimes in surprisingly shallow and often turbulent water. Although fishes living entirely in this habitat would not be expected to be ciguatoxic, Halstead and Schall (1958) reported one specimen of this species as weakly toxic from Malden Island.

Two specimens, 354 and 360 mm SL, 1.1 and 1.6 kg, from Enewetak were tested. Both proved to be nontoxic.

The stomach contents of seven specimens from Enewetak, 235-360 mm SL, and one from Ducie Atoll, Pitcairn Group (420 mm SL, 2.3 kg) were examined. Three had eaten crabs (grapsids in two,

FIGURE 19.—*Epinephelus socialis*, 222 mm SL, Po: ape, Caroline Islands.

including *Percnon*, and the xanthid crab *Eriphia sebana* was found in the third); one of 330 mm contained an octopus (60% by volume) and a prejuvenile acanthurid fish; one of 354 mm contained an acanthurid 165 mm SL. The remaining stomachs were empty.

Epinephelus tauvina (Forsskål) (Figure 20): The name *E. tauvina* has often been applied to a huge grouper for which the name *E. lanceolatus* seems correct. Though the true *E. tauvina* can attain moderately large size (to perhaps 800 mm SL or more), it is not a giant species. Schultz in Schultz and collaborators (1953) described this fish as *E. elongatus* from the Marshall Islands, Mariana Islands, Phoenix Islands, and Samoa Islands, and Smith and Smith (1963) named it *E. salonotus* from the Seychelles. Katayama (1960) and Randall (1964) showed that *E. tauvina*, described from the Red Sea, is the senior synonym. This species may be confused with other dark-spotted groupers such as *E. merra* Bloch and *E. hexagonus* (Bloch and Schneider), particularly when it is small. It is differentiated from them in having 15 instead of

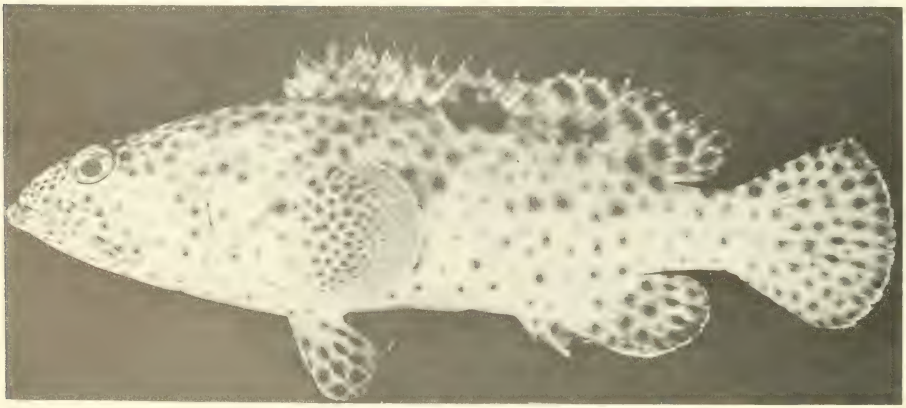


FIGURE 20.—*Epinephelus tauvina*, 252 mm SL, Enewetak, Marshall Islands.

16 soft rays in the dorsal fin, a total of 27-30 gill rakers, instead of 20-27, and a more elongate body.

Epinephelus tauvina is not very common in the Marshall Islands. It may be found in both lagoon and outer reef environments.

Six specimens from Enewetak, 324-434 mm SL, 0.45-2.54 kg, were tested. Four were nontoxic, and one each was poisonous at the 1 and 2 levels. One specimen from Bikini, 400 mm SL, was nontoxic, while a second, 450 mm SL (2.3 kg), gave a mongoose test of 3.

Randall and Brock (1960) found food in the stomachs of 3 of 12 specimens (identified as *E. elongatus*) collected in the Society Islands. All had eaten fishes; in addition, one stomach contained a crab chela.

Thirty-four specimens, 204-500 mm SL, from Enewetak, Society Islands, Line Islands, Cook Islands, Rapa, and the Red Sea were examined for food. Nineteen had empty stomachs, one contained a crab, and the rest had eaten fishes, of which one could be identified to species (*Adioryx lacteoguttatus*) and three to family (Pomacentridae, Holocentridae, and Mullidae).

Plectropomus leopardus (Lacepède) (Figure 21): This is the largest and most common of four groupers of the genus *Plectropomus* in the Marshall Islands. The genus is readily distinguished from other Micronesian serranid genera in having eight dorsal spines and large canine teeth in the jaws; also the body is more elongate than most other groupers. *Plectropomus leopardus* is reddish with small dark-edged blue spots and an emarginate caudal fin.

This species is among the worst offenders in Oceania for causing ciguatera. Halstead (1967) listed it as poisonous from Jaluit in the Marshall Islands and in the Tuamotus. He cited 10 papers that have reported on its toxicity in the Pacific, among them Randall (1958) who noted it as the most toxic of the groupers in Tahiti and reported his own poisoning from the Tuamotus.

Thirty-one specimens were collected at Enewetak for ciguatoxin content, mainly by spearing. The fish ranged from 426 to 790 mm SL and weighed from 1.8 to 11.8 kg. Twelve were nontoxic, six were poisonous at the 1 level, eight at 2, four at 3, and one (520 mm SL) was a 5. One specimen (8.2 kg) from Bikini was nontoxic.

Randall and Brock (1960) recorded the food of seven specimens from the Society Islands: four had empty stomachs and the rest had eaten fishes.

Thirty-seven specimens 426-790 mm SL were collected for food-habit study from Enewetak, Society Islands, and Okinawa. Fifteen had empty stomachs, and the rest contained fishes. Five had eaten parrotfishes (one grouper, 702 mm SL, contained a *Scarus gibbus* 313 mm SL). A 643 mm fish contained two acanthurids, one of which was a *Ctenochaetus striatus* 153 mm SL. A 705 mm grouper had eaten a labrid, *Cheilinus undulatus*, 270 mm SL. Two others had groupers in their stomachs, a 659 mm fish contained *E. tauvina* 267 mm SL, and a 790 mm fish contained a half-digested *Epinephelus* sp.

Plectropomus melanoleucus (Lacepède) (Figure 22): This distinctively colored grouper, white with

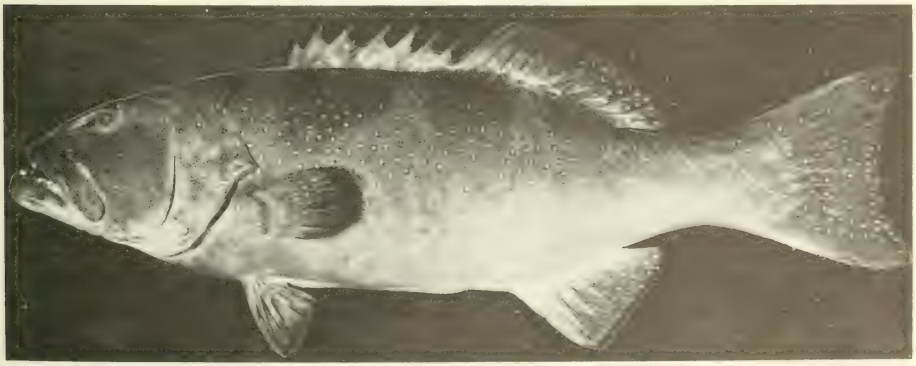


FIGURE 21.—*Plectropomus leopardus*, 513 mm SL, 3.4 kg, Enewetak, Marshall Islands.

FIGURE 22.—*Plectropomus melanoleucus*, 492 mm SL, Enewetak, Marshall Islands.

black saddlelike bars, scattered small blue spots, and yellow fins has been regarded as a color phase of *P. maculatus* (Bloch) by a number of authors from Boulenger (1895) to Smith and Smith (1963). *Plectropomus melanoleucus*, however, is a valid species. In addition to color, it differs from *P. maculatus* (and *P. leopardus* and *truncatus*) by usually having 17 instead of 16 pectoral rays.

This species is rare in Oceania. Only a single specimen, 506 mm SL, 2.95 kg, was taken at Enewetak during the ciguatera survey. Its viscera produced a reaction of 2 when fed to a mongoose.

Its stomach was empty.

Plectropomus truncatus Fowler (Figure 23): Like *P. leopardus*, this grouper has dark-edged blue spots, but the spots are larger in fishes of about the same size. The best field character to distinguish this species is its truncate caudal fin.

One specimen (384 mm SL, 1.45 kg) from Enewetak produced a ciguatoxic reaction of 2; its stomach was empty.

Hiatt and Strasburg (1960) reported one of three specimens of this grouper collected at Enewetak with a holocentrid fish in its stomach.

Variola louti (Forsskål) (Figure 24): This colorful grouper is yellowish brown to orange, profusely spotted with blue or pink (blue from shallow water, pink in deeper water), with broad zones of yellow posteriorly on the median and pectoral fins. Apart from color, it is readily distinguished by its deeply concave caudal fin. It is usually found on outer reefs at depths >15 or 20 m.

FIGURE 23.—*Plectropomus truncatus*, 350 mm SL, Enewetak, Marshall Islands.

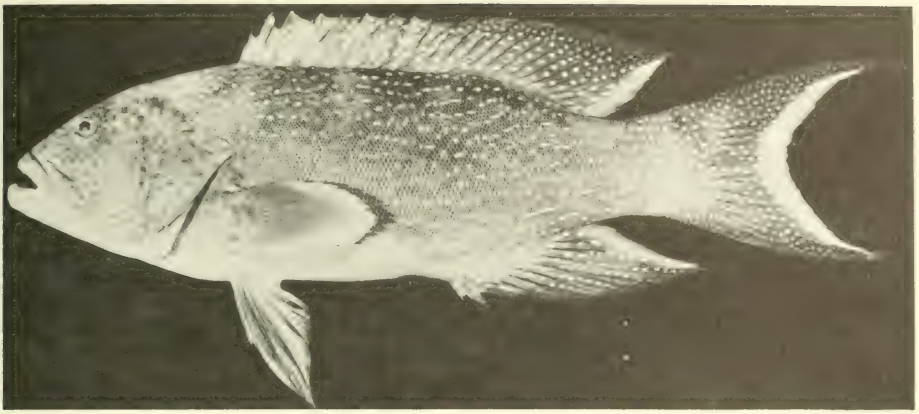


FIGURE 24.—*Variola louti*, 273 mm SL, Enewetak, Marshall Islands.

Variola louti is well known as a cause of ciguatera. In Mauritius it is prohibited from sale in fish markets. Toxicity there has been reported by Wheeler in Wheeler and Ommanney (1953).

Nineteen specimens were obtained for testing at Enewetak. They ranged from 352 to 418 mm SL and weighed from 1.1 to 2.2 kg. Thirteen were nontoxic, four gave a mongoose test of 1, and two a test of 3. Two from Bikini, 292 and 420 mm SL, were nontoxic.

Randall and Brock (1960) opened seven stomachs of the species from the Society Islands. Five were empty and two contained digested fishes. Hiatt and Strasburg (1960) found a juvenile unicornfish, *Naso* sp., in the stomach of one of two specimens from Bikini. Helfrich et al. (1968) examined the stomach contents of 44 specimens from the Line Islands. They found fishes, including acanthurids, balistids, and muraenids, in 80% of the stomachs, and crustaceans in 11%.

For the present food-habit study 44 specimens were examined. These ranged from 180 to 560 mm SL (largest weighed 5.45 kg). They were caught at Enewetak, Bikini, Line Islands, Tahiti, Rarotonga, Pitcairn Group, Rapa, and Tutuila. Twenty had empty stomachs. One contained a crab, one a spiny lobster, and the rest had eaten fishes, of which the following were identified at least to family: *Adioryx* sp. (120 mm specimen in a 295 mm grouper), *Scorpaena* sp. (28 mm specimen in a 235 mm grouper), *Parupeneus trifasciatus* (a 53 mm transforming specimen in a 470 mm grouper), juvenile *Chaetodon* sp., *Anampses caeruleopunctatus* (identified from scales), *Scarus sordidus* (140 mm specimen in a 375 mm grouper), and a pomacentrid.

Lutjanidae (Snappers)

Aprion virescens Valenciennes (Figure 25): This elongate snapper has been reported as poisonous from a number of Pacific localities, including the leeward Hawaiian Islands (Halstead 1967). Halstead did not list any Indian Ocean localities. It may therefore be worthy of note that the author incurred a mild case of ciguatera from eating a fish of this species at Mauritius. Also he was informed that poisoning is known from nearby Réunion.

Aprion virescens is a roving carnivore of open water but often found within or near reef areas, both in atoll lagoons and in outer reef zones. It is difficult to approach underwater; most of the specimens were obtained by hook and line, often while trolling.

Eleven specimens, 435-622 mm SL (1.6-5.2 kg), from Enewetak were tested. Eight were nontoxic, one (589 mm) gave a reaction of 1, one (622 mm) was a 3, and one (620 mm) a 4.

Eight were taken at Bikini ranging from 406 to 685 mm SL (1.8-5.4 kg). All, exept one of 457 mm SL which produced a mongoose reaction of 1, were nontoxic.

Ommanney in Wheeler and Ommanney (1953) reported on the analysis of stomach contents of 80 *A. virescens* from the Mauritius-Seychelles region. Forty-four of these were empty. The stomachs of

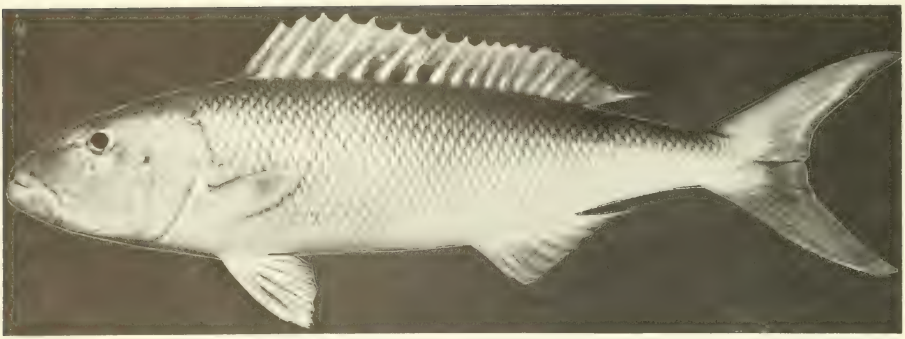


FIGURE 25.—*Aprion virescens*, 503 mm SL, 2.5 kg, Nuku Hiva, Marquesas Islands.

21 contained fishes; 6 had fishes and macroplankton; 5 had only macroplankton; and 4 contained cephalopods. Among the fishes taken from the stomachs were scarids, ostraciids, siganids, a bothid, and *Caesio coerulaureus*.

Talbot (1960) reported on 259 specimens caught by handline and surface lure on the east African coast which ranged from 202 to 800 mm SL (weight to 11.3 kg). He presented a diagram of the relative abundance of food organisms for this fish as follows: fishes 49%, plankton 17%, cephalopods 14%, and crustaceans exclusive of plankton (mainly portunid crabs) 12%. He did not indicate how many specimens had empty stomachs.

The stomachs of 15 specimens from the Marshall Islands and 1 from Hawaii were examined. Ten were empty. Four contained fishes; (one prey fish identified as *Scarus* sp.); one *A. virescens* (481 mm SL) had also eaten an octopus (one-third stomach volume). A 457 mm fish contained a 10 mm calappid crab, and one of 650 mm a stomatopod.

Lutjanus bohar (Forsskål) (Figure 26): This red snapper has been implicated more frequently in ciguatera than any fish of the Indo-Pacific region. It is probably the species which sickened the crew of Captain Cook in the New Hebrides in 1774 (Banner 1965). Its toxicity has also been reported under the junior synonym *Lutjanus coatesi* Whitley. This species occurs along seaward reefs and in passes. It is more common around atolls and low coral islands than high islands (Randall and Brock 1960). It is especially abundant in the Line Islands. Reef fishes became highly toxic there during and immediately after World War II; the toxicity declined in the early 1960's (Banner and Helfrich 1964). When the toxicity was high, *L. bohar* from these islands was used for the chemical and pharmacological work on ciguatoxin at the University of Hawaii (replaced by *Lycodontis javanicus* from Johnston Island in later years). It was the species used by Banner et al. (1966) to demonstrate the long periods of retention of ciguatoxin in the tissues of poisonous fishes when removed from the source of the toxin.

The toxicity of 95 specimens from Enewetak from 430 to 635 mm SL (2.5-7.5 kg) was tested. Fifty-six were nontoxic; 22 gave a mongoose test of 1; 11 were 2, 5 were 3, and 1 (533 mm) was a 5.

From Bikini 143 specimens which ranged from 330 to 760 mm SL were tested. Of these, 112 were nontoxic, 15 were 1, 8 were 2, 6 were 3, and 2 gave a mongoose test of 4.

From the atoll of Rongelap (lat. 11° N, long. 167° E) in the Marshall Islands we obtained 12 specimens of *L. bohar* which weighed from 3.2 to 9.1 kg. Eight of these were nontoxic, two gave a reaction of 2, one was a 3, and one a 5.

Hiatt and Strasburg (1960) found fragments of fish in one of two specimens of *L. bohar* from Bikini. Talbot (1960) examined 854 specimens from the East African coast; 58% had empty stomachs. Fishes composed 62% of the food material, crustaceans 24%, and mollusks 8%. Helfrich et al. (1968) determined the diet of 2,276 specimens from Palmyra and Christmas Islands in the Line Islands; 21.4% of these were empty. Fishes dominated the stomach contents (48.7% by volume at Palmyra and 65.4% at Christmas), of which acanthurids were the most common among those identified. Mollusks represented 19.1% by volume

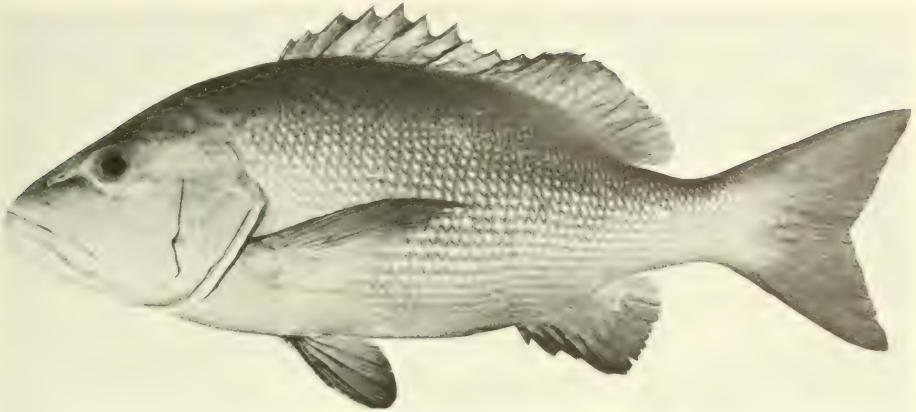


FIGURE 26.—*Lutjanus bohar*, 520 mm SL, 4.9 kg, Ulithi, Caroline Islands.

of the total food material at Palmyra and 18% at Christmas. Crustaceans (principally decapod megalops) composed 15.4% of the food among Palmyra fish and 13.3% of Christmas Island specimens.

The stomachs of 121 adult specimens of *L. bohar* from the Marshall Islands, 330-635 mm SL, most of which were taken by hook and line, were examined. Eighty-six were empty. Of those with identifiable food, 76.2% contained fishes (including *Lycodontis* sp., *Cephalopholis urodelus*, *Archamia* sp., *Lethrinus variegatus*, *Scarus* sp., and *Ostracion* sp.), 10.8% had eaten crabs (including portunids), 8.7% contained octopus, and 4.3% shrimps.

Lutjanus fulvus (Schneider) (Figure 27): The names *L. vaigiensis* (Quoy and Gaimard) and *L. marginatus* (Cuvier) are junior synonyms that have often been used for this snapper. It is yellowish on the body, the head gray, the caudal fin reddish black with a narrow white posterior border; the dorsal fin is reddish and the anal and pelvic fins yellow. It is a small inshore species, abundant throughout the Indo-West Pacific. It is found more often in sheltered than exposed environments. Hiyama (1943:48-49, pl. 6, fig. 17) reported that Marshallese natives informed him that this fish (which he identified as *L. flavipes* Valenciennes), rarely causes ciguatera; when it does, the cases are light. Halstead (1967:98, pl. 68, fig. 4) listed it among the ciguatoxic fishes [misidentified as *L. janthinuropterus* (Bleeker)].

Two specimens from Enewetak, 207 and 217 mm SL, were nontoxic.

Randall (1955a) examined the stomachs of six specimens taken with rotenone at Tarawa, Gilbert Islands. One had eaten a small holothurian, one a brachyuran crab, and two contained fishes that were probably prior victims of the ichthyocide. Hiatt and Strasburg (1960) analyzed the stomach contents of six juveniles from Arno, Marshall Islands; they reported the following food items: crabs, fishes, amphipods, shrimps, and stomatopods. Randall and Brock (1960) examined 50 specimens which had food in their stomachs; 54.3% of these contained crustaceans (mainly crabs) and 42.4% fishes. Helfrich et al. (1968) collected 51 specimens from Palmyra for food-habit study. The dominant food items were mugilid, mullid, and pomacentrid fishes; crustaceans made up the next most frequent organisms of the diet.

For the present study 44 specimens 182-250 mm SL were collected in the Marshall Islands, Mariana Islands, and Caroline Islands. Thirty-one of these had empty stomachs. Of those with food, 68.4% had eaten crustaceans (nearly all crabs, mainly calappids) and 31.6% fishes.

Lutjanus gibbus (Forsskål) (Figure 28): This snapper is also reddish like *L. bohar*, but it does not attain such large size. The dorsal profile of adults, beginning with the nape, is highly convex, which is the basis for the specific name. Schultz in Schultz and collaborators (1953) stated, "This species was taken only in moderately deep water.

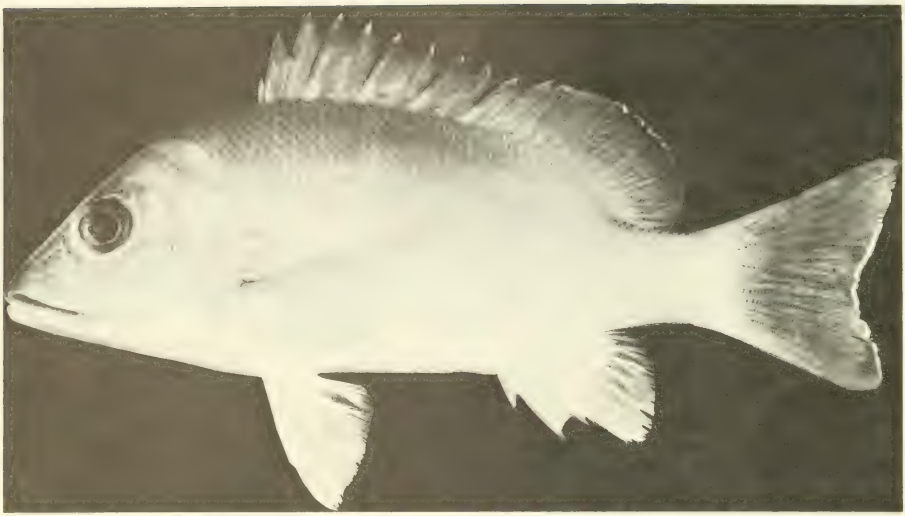


FIGURE 27.—*Lutjanus fulvus*, 215 mm SL, Enewetak, Marshall Islands.

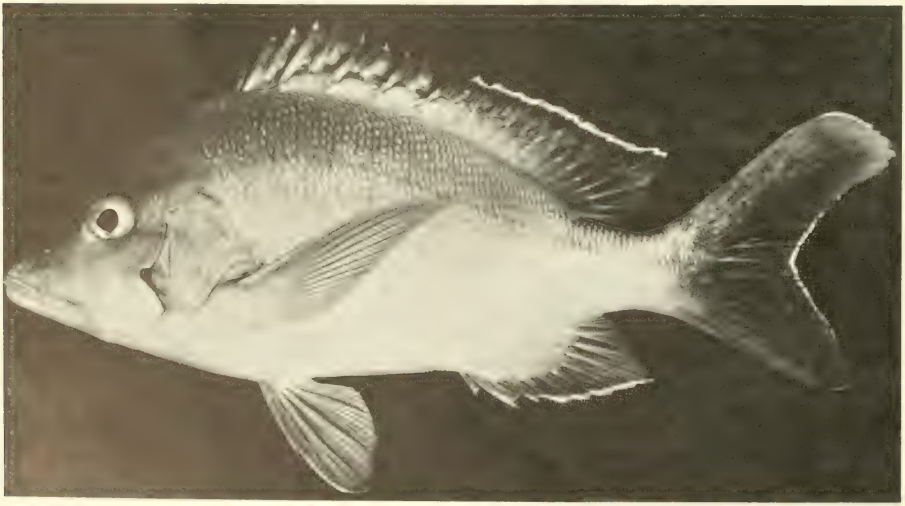


FIGURE 28.—*Lutjanus gibbus*, 291 mm SL, Palmyra, Line Islands.

It did not occur over the shallow parts of the reefs." Talbot (1960), on the other hand, wrote in reference to *L. gibbus* in east Africa, "It was only found in shallow water of from 3 to 8 fathoms." Actually, the species may occur either in the shallows or at moderate depths, but in the Marshall Islands, at

least, it is usually encountered in water of 20 m or more. Though mainly found on the outside of sea reefs and in passes, it may also occur in lagoons. It is often observed in large aggregations.

Thirty-one specimens of *L. gibbus* from Enewetak 302-375 mm SL (largest 1.8 kg) were collected. Twenty-one of these fishes were nonpoisonous; five were rated as 1, two were 2, and three ranked 3 by the mongoose test.

Thirty-five specimens from Bikini, 279-385 mm SL, were tested. All but three were nontoxic; the three toxic fish produced a mongoose reaction of only 1.

Randall and Brock (1960) collected 23 specimens in the Society Islands of which only 9 had food in their stomachs (5 of these were juveniles). The four adults contained fishes, crabs, and unidentified crustaceans. Hiatt and Strasburg (1960) examined 43 specimens (175-260 mm SL) from the Marshall Islands of which 10 had empty stomachs. Crustaceans were the main food, especially crabs (60% contained xanthids and 17% portunids); Amphineura were found in 13% of the stomachs. *Octopus*, *Natica*, *Ptychodera*, small holothurians, polychaetes, sipunculids, and fish *Apogon* were all found in 4% of the stomachs. Talbot (1960) reported on the capture of 121 specimens. He wrote, "Foods eaten were mainly crustaceans, including crabs and Penaeid prawns. Small coral fishes were also occasionally taken." Helfrich et al. (1968) found food in 36 of 45 stomachs of adults from the Line Islands; fishes were the main item of diet, with crustaceans the second most abundant. [Fishes included unidentified eels, acanthurids, and *Pomacentrus nigricans* (= *Stegastes nigricans*).] Most crustaceans were brachyuran crabs, but there were also alpheid shrimps and slipper lobster. Mollusk remains were mainly prosobranchs, but opisthobranchs and cephalopods were also found. Sea urchins were the most common of the miscellaneous invertebrates composing the rest of the stomach contents.

During the present study the stomachs of 51 specimens from the Marshall Islands, 260-419 mm SL, were examined. Twenty-seven were empty. Of those with food, 40% had eaten crabs, 26% fishes (including *Pseudocheilinus* sp. and *Adioryx microstomus*), 17% echinoids (including *Eucidaris* sp. and *Heterocentrotus mamillatus*), 12% ophiuroids (including *Ophiocoma erinaceus*), 2.1% alpheid shrimps, 2.1% octopus, and 0.3% gastropods.

Lutjanus monostigmus (Cuvier) (Figure 29): This species, named from the blackish spot usually present on its side (on lateral line), is capable of causing severe cases of ciguatera. Belotte (1955) gave the case history of an American who was in a coma 3 days after eating this snapper in Tahiti; the author also interviewed this man. The sale of this species in Tahiti, where it is called "taivaiva," (Randall 1972) is forbidden. It is found in reef environments from shallow water to moderate

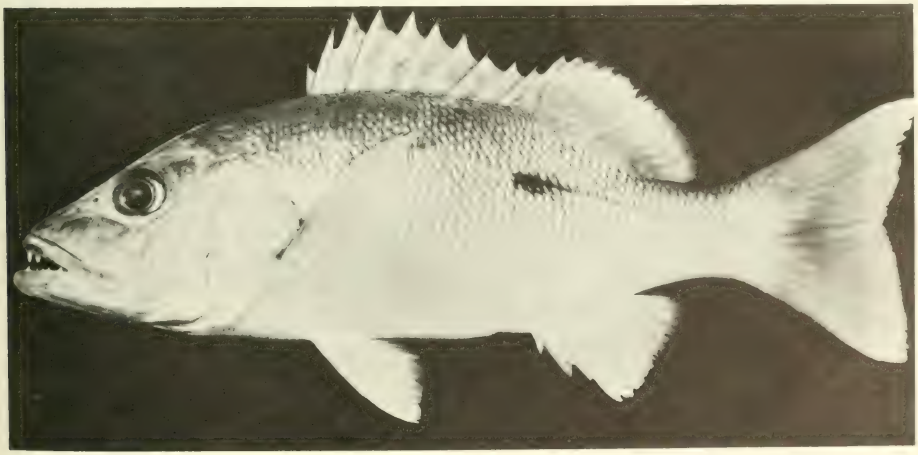


FIGURE 29.—*Lutjanus monostigmus*, 249 mm SL, Florida Island, Solomon Islands.

depths, especially where there is deep shelter. Not infrequently it is encountered in small aggregations. Adults are wary, hence difficult to spear.

Only three specimens were obtained from Enewetak, 310-420 mm SL (0.8-1.6 kg), for testing of toxicity. One was nontoxic, one was 1, and one a 2.

Five specimens, 400-445 mm SL, were collected in Bikini. Four were nontoxic; the largest gave a mongoose reaction of 1.

Randall and Brock (1960) opened 32 stomachs of adults of this species, of which 18 were empty. Those with full stomachs all contained fishes, among them *Decapterus pinnulatus*, *Selar crumenophthalmus*, and *Ctenochaetus striatus*. Hiatt and Strasburg (1960) found a goatfish in the stomach of one of three specimens from Enewetak; the other two were empty. Talbot (1960) collected 18 specimens off east Africa. He reported fish remains (including a mullid and a labrid) in most stomachs; penaeid prawn remains were also found. Helfrich et al. (1968) examined 29 specimens from the Line Islands. They found fishes in 92% of the stomachs and crustaceans (stomatopod larvae and one slipper lobster) in 23%.

For the present food-habit study 41 specimens of *L. monostigmus* were examined from the Marshall Islands, Society Islands, Line Islands, and Samoa Islands. Twenty-three had empty stomachs. Of those with food, 92% by volume had eaten fishes (including the holocentrid *Adioryx microstomus*, acanthurids, and a balistid), and 8% crabs (including a portunid).

Macolor niger (Forsskål) (Figure 30): Although not previously reported as poisonous, this lutjanid fish attains moderate size, is a reef-dweller, and carnivorous; this would seem to have the potential for causing ciguatera. A total of 25 adults, 403-445 mm SL (2.3-2.95 kg), were taken, all from Enewetak, and mainly from explosive stations in the lagoon. Twenty-three were nontoxic and two gave a reaction of 1 on the feeding of liver and viscera to mongooses.

The stomachs of eight adult specimens taken at 9:00 a.m. at Enewetak were examined. All were empty. The large eyes of this species is suggestive of nocturnal habits, and the numerous (about 72) long gill rakers would seem to indicate at least some feeding on zooplankton (perhaps more important in smaller individuals than large adults). Some of the specimens were caught by hook and line baited with fish. Hiatt and Strasburg (1960) also reported that this species can be caught on a baited hook.

Lethrinidae (Emperors)

Lethrinus amboinensis Bleeker (Figure 31): Following Sato (1978), this emperor is identified as *L. amboinensis*. It lacks characteristic color markings, being light brownish to greenish dorsally

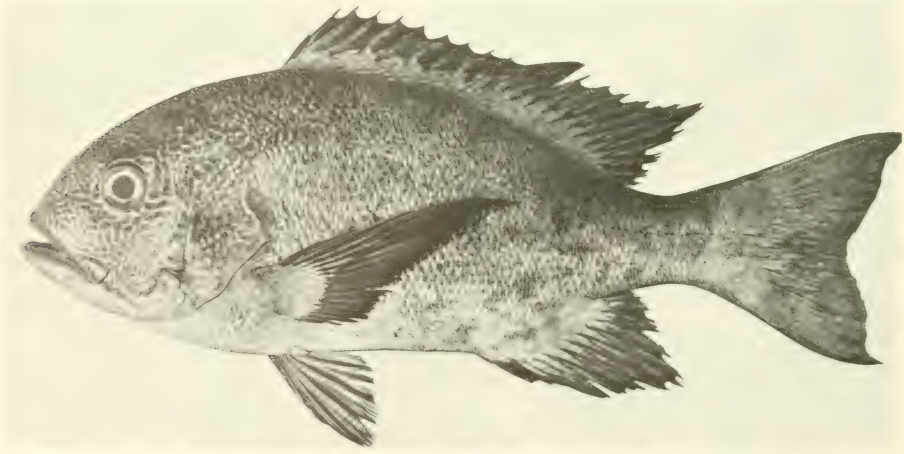


FIGURE 30.—*Macolor niger*, 378 mm SL, Enewetak, Marshall Islands.

FIGURE 31.—*Lethrinus amboinensis*, 294 mm SL, Enewetak, Marshall Islands.

with small dark brown spots and blotches, shading to white ventrally. It is somewhat elongate, the head length greater than the depth; the snout is moderate, its length in adults 1.8-1.0 in head length; the maxilla reaches a vertical a little posterior to the anterior nostril. The teeth along the sides of the jaws are conical.

Twenty-four specimens were taken at Enewetak and nine at Bikini, the largest 310 mm SL. All were nontoxic.

Helfrich et al. (1968) determined the food of 14 specimens of *L. amboinensis* from Palmyra, Line Islands. Fishes were found in 75% of the stomachs, mollusks in 25%, and crustaceans in 17%; all specimens had some sea urchin fragments.

Fish remains were found in one of two stomachs examined at Bikini.

Lethrinus kallopterus Bleeker (Figure 32): This *Lethrinus* is distinctive in having orange fins and blackish spots over occasional scales; the snout is short, the maxilla reaching a vertical at anterior edge of eye. The teeth at the sides of the jaws are nodular (i.e., neither conical nor well-developed molars). It was most often seen in the deeper parts of the atoll lagoons.

A total of 19 specimens were collected at Enewetak for the testing of toxicity. These ranged from 337 to 443 mm SL (1.1-2.7 kg). Fourteen were nontoxic, two produced a reaction of 1, two were 2, and one (368 mm SL) was a 5.

Two specimens, 330 and 457 mm SL, were procured from Bikini; neither was toxic.

The stomachs and intestines of 13 specimens, 330-443 mm SL, from the Marshall Islands were opened. Five of the fish were empty. Four had eaten only echinoids (including *Echinometra mathaei*); one contained mostly echinoids but also the cowrie *Cypraea carneola*; another (the largest) had eaten just the cowrie *C. vitella*; still another had a cowrie in its gut (20% by volume of the food material), and the rest of the food material consisted of crinoids; one specimen contained only a starfish arm.

Lethrinus miniatus (Forster in Bloch and Schneider) (Figure 33): This emperor has an especially long snout (1.6-1.8 in head length of adults). It is primarily gray in color, but can alter its pattern, like many other *Lethrinus*, to one of dark irregular bars and blotches. Often there are two or three bluish streaks on the snout passing anteriorly and diagonally downward from the eye. The teeth on the sides of the jaws are conical. This species was seen in both lagoon and outer reef environments, but mainly in lagoons. It is among the largest of the emperors, reported to attain 1 m.

Of nine adults, 435-530 mm SL (1.8-3.6 kg), which were caught at Enewetak, six were nontoxic, and three gave a reaction of 3.

Twelve specimens from Bikini, 381-635 mm SL, 1.4-7.3 kg, were nontoxic.

Eight of 14 specimens from Enewetak and Bikini had food in their stomachs. Three contained fish remains, one of which (456 mm SL) included a

FIGURE 32.—*Lethrinus kallopterus*, 345 mm SL, Enewetak, Marshall Islands.

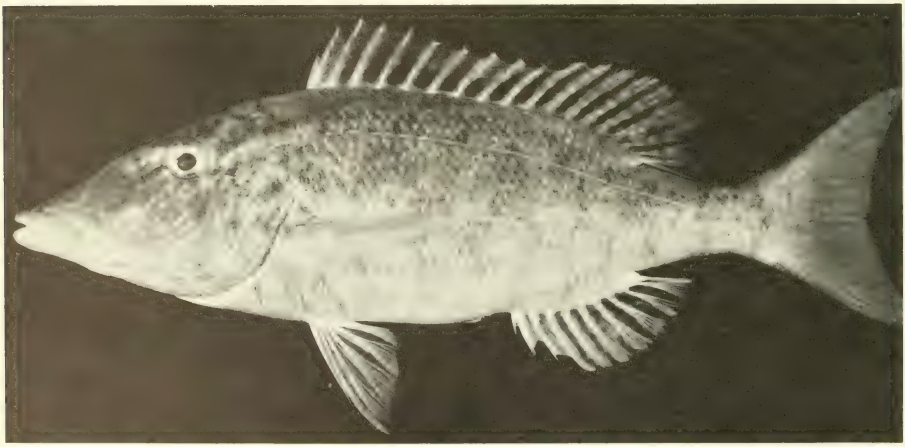


FIGURE 33.—*Lethrinus miniatus*, 430 mm SL, Enewetak, Marshall Islands.

Lethrinus 115 mm SL; the remaining three had eaten crustaceans (stomatopod, crab, and alpheid shrimp).

Lethrinus xanthochilus Klunzinger (Figure 34): This emperor is one of the more slender species of *Lethrinus* (depth 3.1-3.3 in SL). The interorbital space is nearly flat. The teeth on the sides of the jaws are conical. The upper lip is orange-yellow, and there is a red spot at the upper pectoral base. It is found more in lagoons than exposed reef habitats; it will venture into shallow water.

Two specimens, 445 and 550 mm SL (smallest 1.7 kg, largest not weighed), were collected at

FIGURE 34.—*Lethrinus xanthochilus*, 395 mm SL, Fanning Island, Line Islands.

FIGURE 35.—*Monotaxis grandoculis*, 220 mm SL, Enewetak, Marshall Islands.

Enewetak; two, 305 and 432 mm SL, were taken at Bikini. All were nontoxic.

The stomach and gut contents of these four specimens and one of 466 mm from the Society Islands were examined. One fish contained crushed echinoids, one the remains of a calappid crab, one a digested fish, another both crab and fish remains, and one (the largest) a freshly ingested fish (probably from a rotenone station).

Monotaxis grandoculis (Forsskål) (Figure 35): *M. grandoculis* has been classified in the past principally in the Sparidae or Lutjanidae, but is now recognized as a lethrinid. It is readily distinguished by its large eyes, short blunt snout, and single row of well-developed molariform teeth along the side of the jaws. It occurs in a wide variety of reef habitats. Adults are difficult to approach underwater. This fish feeds mainly on in-

vertebrates with calcareous or chitinous hard parts. Although rarely implicated in serious cases of poisoning, it is capable of being ciguatoxic. Halstead (1967) listed 11 references attesting to its toxicity.

Five specimens, 277-362 mm SL (0.73-1.6 kg), from Enewetak were tested for toxicity. Four were nontoxic and one gave a reaction of 1 from the mongoose feeding.

Randall (1955a) reported on the gut contents of two specimens, 158 and 160 mm SL, from the Gilbert Islands; these consisted mainly of crushed shells of small mollusks and sea urchins. Hiatt and Strasburg (1960) examined the contents of the digestive tracts of eight specimens, 195-220 mm SL, from the Marshall Islands. One fish was empty. Crushed gastropods (including *Atys* sp. and *Cerithium* sp.) were found in all stomachs, pelecypods in 71%, crabs in 42%, hermit crabs in 28%, and spatangids and polychaetes each in 14%. Hobson (1974) collected five specimens in Hawaii. He found the principal prey, in order of importance in the diet, to be prosobranch gastropods, ophiuroids, echinoids, opisthobranch gastropods, and pagurid crabs.

Forty-eight specimens of *M. grandoculis,* 155-440 mm SL, were collected from the Marshall Islands, Line Islands, Cook Islands, Society Islands, Pitcairn, Hawaiian Islands, New Guinea, and the Red Sea for the study of food habits. Unless fish of this species are captured during the night or very early morning hours, their stomachs are nearly always empty. Occasional feeding by *M. grandoculis* does occur during the day, as indicated by Hiatt and Strasburg's (1960) observation of its "blowing" away sand to expose fossorial forms. Also one specimen taken at 2 p.m. during the author's survey had the remains of a freshly ingested crab in its stomach. Five of the fish collected in late afternoon hours had completely empty digestive tracts. The remaining fishes contained, on a volume basis, 39.4% gastropods, 18.9% crabs, 16.8% pelecypods, 13.9% echinoids (principally *Echinometra* and spatangoids such as *Clypeaster*), 6.1% pagurid crabs, 1.7% ophiuroids, 1.2% polychaetes, 1.0% unidentified worms, 0.7% fishes, and 0.3% foraminifera.

Kyphosidae (Sea Chubs)

Kyphosus cinerascens (Forsskål) (Figure 36): This chub may be distinguished from the other *Kyphosus* by the high soft portion of the dorsal fin (longest dorsal spine contained about 1.8 times in longest soft ray). It occurs in lagoon or outer reef areas and is often seen in loose aggregations. It is associated with hard substratum for its algal food, generally in the vicinity of crevices or caves with more than one entrance. Bartsch et al. (1959) reported this species as toxic from Majuro, Marshall Islands, but their data and the few other records of

FIGURE 36.—*Kyphosus cinerascens,* 234 mm SL, Enewetak, Marshall Islands.

toxicity would seem to indicate that it is only marginally a cause of ciguatera.

Of two specimens from Enewetak, 356 and 364 mm SL, 1.8 kg, one was nonpoisonous and the other toxic at level 1.

Hiatt and Strasburg (1960) found benthic algae in the stomachs of three of four specimens examined in the Marshall Islands. Hobson (1974) reported algae in three stomachs from Hawaii; however, *K. cinerascens* apparently does not occur in the Hawaiian Islands (though two other species are present).

Three specimens, 330-364 mm SL, from Enewetak were opened. The stomach of one was empty, and the other two contained benthic algae. The algae of one were identified by Tsuda[8] as the reds *Gelidium pusillum*, *Champia parvula*, and *Leveillea jungermannoids* (90%) and the brown *Sphacelaria tribuloides*.

Carangidae (Jacks)

Caranx ignobilis (Forsskål) (Figure 37): This steep-headed jack is the largest species of the genus. Bagnis et al. (1972) stated that it can attain a length of 2 m and a weight of 80 kg. It can be differentiated from other Marshall Islands species by the absence of scales on the thorax except for a small median patch. Like other large carangids, it is a roving carnivore; it may be encountered anywhere in the atoll environment including water surprisingly shallow for such a large fish.

The author interviewed a man and wife in Moorea who were poisoned from eating the liver of a large individual of this species (estimated 1.5 m) which overturned their canoe in the long struggle to catch it. Both were very ill with ciguatera, the man comatose for several hours.

Five specimens, 573-920 mm FL, 3.6-16.3 kg, were obtained at Enewetak for the testing of toxicity. Three gave a 0 reaction and two a reaction of 1. Two specimens from Bikini, 635 and 1,105 mm FL, 4.5 and 27.3 kg, were nontoxic.

A total of 14 specimens were collected for food-habit study from the Marshall Islands, Line Islands, Hawaiian Islands, Pitcairn Group, and the Marquesas. Seven stomachs were empty, and the rest contained the digested remains of fishes, of which only one could be identified to species, the surgeonfish *Zebrasoma flavescens*. One stomach-content fish was a scorpaenid, and another (from a jack of 1,217 mm FL, 37.5 kg) a scarid.

Caranx lugubris Poey (Figure 38): The black jack is a circumtropical species with a well-earned reputation for causing ciguatera. Although the

[8]Roy T. Tsuda, Marine Laboratory, University of Guam, Box EK, Agaña, Guam 96910, pers. commun. 1972.

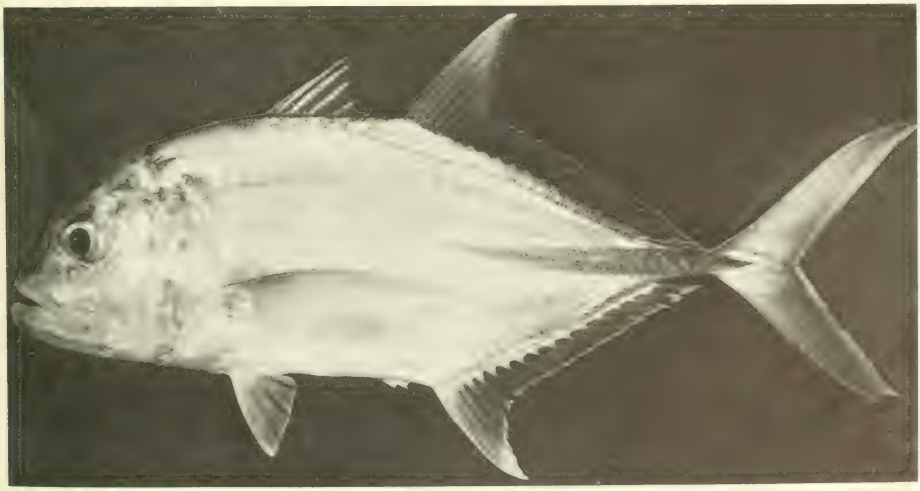


FIGURE 37.—*Caranx ignobilis*, 378 mm FL, Fanning Island, Line Islands.

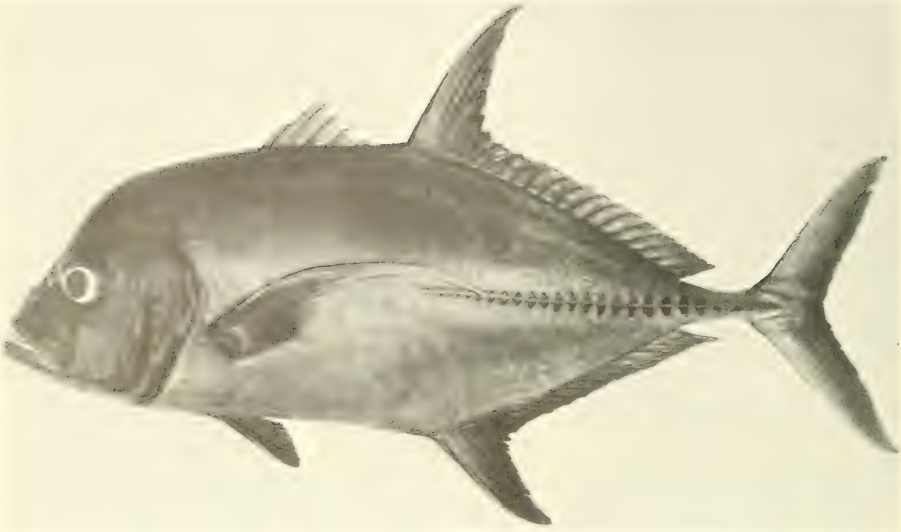


FIGURE 38.—*Caranx lugubris*, 557 mm FL, 3.1 kg, St. John, U.S. Virgin Islands.

dark color (especially on the scutes) and distinctive configuration generally permit identification, the fully scaled breast will provide separation from *C. ignobilis*, the low number of scutes on straight portion of lateral line (26-33) from *C. melampygus*, and the high gill raker count (18-20 on lower limb) from *C. sexfasciatus*. This species is found mainly around oceanic islands and is nearly always encountered in the clear water of outer reef environments.

Fifteen specimens were obtained at Enewetak for testing. These ranged from 488 to 910 mm FL and weighed from 2.5 to 15.5 kg. Eleven were nonpoisonous, two gave reactions of 1, one was a 2, and one a 3. No specimens were collected at Bikini.

Randall (1955a) reported a fish in one of two specimens collected in the Gilbert Islands and Randall (1967) found fishes in two of six specimens from the Caribbean Sea.

For the present food-habit study, 10 specimens were obtained from Enewetak and Henderson Island in the Pitcairn Group. Four had empty stomachs, and the remaining six contained the remains of fishes, one of which was a labrid.

Caranx melampygus Cuvier and Valenciennes (Figure 39): This is the most abundant jack of the genus in Oceania; it is widespread in the tropical and subtropical Indo-West Pacific and ranges to the eastern Pacific as well. It is irridescent blue along the back and median fins in life with a scattering of small blackish spots on the head and body except ventrally. The chest is completely scaled, and there are 38-44 scutes in the straight portion of the lateral line.

Thirty specimens were collected at Enewetak, 417-722 mm FL, 1.4-6.8 kg, for the assay of ciguatera. Twenty-four were nontoxic, four gave a reaction of 1, one was a 2, and one a 3.

Six specimens from Bikini, 394-686 mm FL, 1.8-6.6 kg, were nontoxic.

Randall (1955a) examined the stomach contents of four specimens from the Gilbert Islands. Two contained many small freshly ingested fishes which were probably the result of a rotenone station kill. Of the other two which were speared, one contained the anthiine fish *Mirolabrichthys tuka* (= *Anthias pascalus*). Hiatt and Strasburg (1960) found fish in the stomachs of two from the Marshall Islands, one of which was identified as *Trachurops* (= *Selar*) *crumenophthalmus*. Hobson (1974) examined the stomach contents of six specimens from Hawaii. One contained larval fishes and mysids, a second had fish and shrimp remains, and three contained well-digested fragments at least one of which was fish.

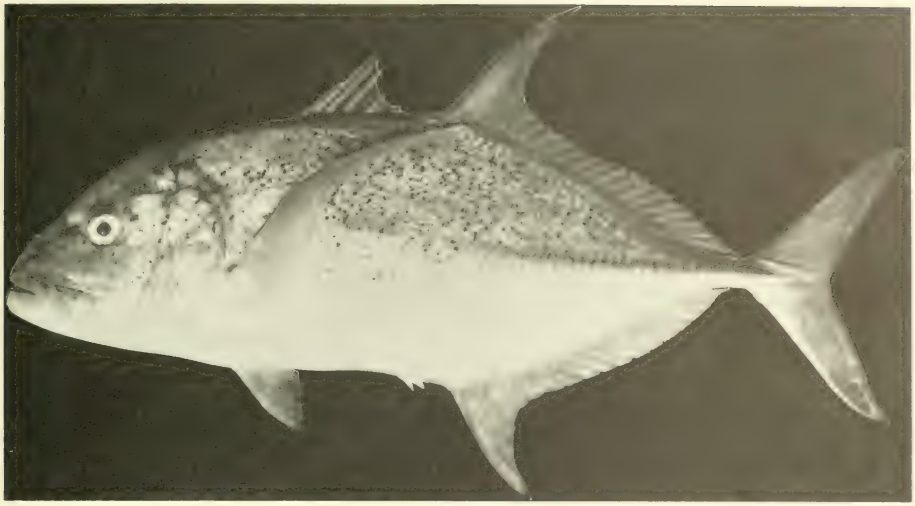


FIGURE 39.—*Caranx melampygus*, 498 mm FL, 1.9 kg, Sanganeb Atoll, Red Sea.

Sixty-one specimens, 298-722 mm FL, from the Marshall Islands, Hawaiian Islands, Line Islands, Marcus Island, Solomon Islands, and the Red Sea were collected for stomach-content study. Seventeen stomachs were empty. All the others contained the digested remains of fishes, though one had, in addition, a squid pen. The following fishes were identified from the stomach material: eel, *Anthias thompsoni*, *Caranx* sp. (90 mm FL in a 520 mm *C. melampygus*), *Priacanthus cruentatus*, *Cirrhitops fasciatus*, *Caesio* sp., *Parupeneus* sp., *P. trifasciatus*, *Pomacentrus pavo*, *Chromis caerulea*, labrid, *Thalassoma purpureum*, *Pterelеotris microlepis*, *Caracanthus unipinnus*, *Acanthurus triostegus*, acronurus stage of acanthurids (in two stomachs), and a subadult acanthurid.

Caranx sexfasciatus Quoy and Gaimard (Figure 40): This jack, which ranges from the Red Sea to eastern Oceania, is closely related to *C. hippos* of the Atlantic. It is usually seen in small schools, but is not common in the Marshall Islands. It is more elongate than the *Caranx* spp. discussed above, and it has a larger eye. The lower-limb gill raker count is 15-17. The scutes are blackish, there is a small black spot at the upper end of the gill opening, and the soft dorsal and anal fins are tipped with white. The dark bars of the young are the basis for the specific name.

Only two specimens were caught at Enewetak, 496 and 700 mm FL, 2.3 and 4.6 kg. Both were nontoxic. No specimens were obtained from Bikini.

Ommanney in Wheeler and Ommanney (1953) reported on the stomach contents of specimens caught during a survey of the Mauritius-Seychelles region. Eight specimens contained fish remains, one had squid remains, one had megalops larvae, and nine were empty. A parrotfish and two eels were noted among the stomach contents.

The stomachs of six specimens of *C. sexfasciatus*, 385-700 mm FL, from Enewetak and Tahiti were opened. Five were empty, and one contained well-digested fish remains. (This jack was speared at 11:30 a.m.)

Bagnis et al. (1972) stated that *C. sexfasciatus* is nocturnal. Wheeler and Ommanney (1953) on the other hand, wrote, "It often takes a lure..."; presumably he meant one trolled by day.

Scombridae (Tunas)

Gymnosarda unicolor (Rüppell) (Figure 41): The dogtooth tuna is named for its large conical teeth; it is also unique in having two patches of villiform teeth on the tongue. It lacks dark stripes or spots on the body; the second dorsal and anal fins are

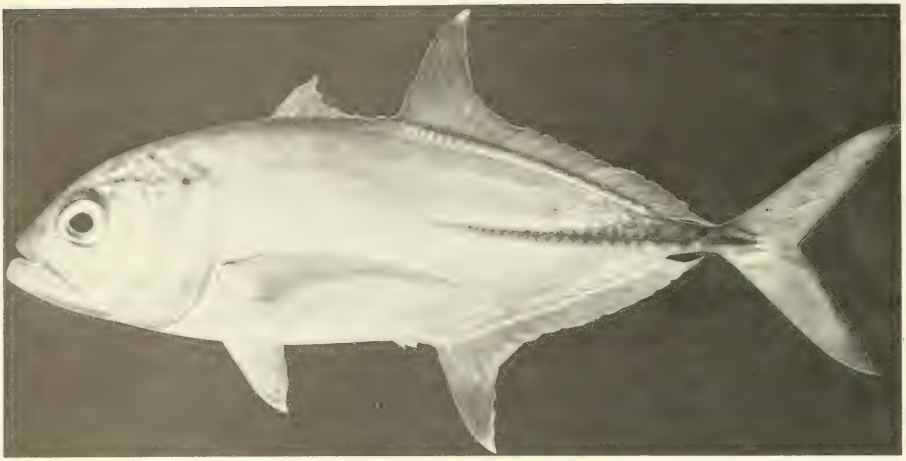


FIGURE 40.—*Caranx sexfasciatus,* 472 mm FL, 1.8 kg, Enewetak, Marshall Islands.

FIGURE 41.—*Gymnosarda unicolor,* 645 mm FL, 3.6 kg, Enewetak, Marshall Islands.

white tipped. A large species, Masuda et al. (1975) recorded it to a length of 2.4 m. Unlike other large tunas, in general, it occurs in relatively shallow coastal water, often around coral reefs, and it readily penetrates the deeper lagoons of atolls.

Thirteen individuals were collected from Enewetak which ranged from 550 to 1,350 mm FL (3.2-35.4 kg). Seven caused no symptoms when liver tissue was fed to mongooses; four produced a reaction of 1, one was a 2, and one a 3.

Three from Bikini, 737-940 mm FL, 6.4-11.8 kg, were nontoxic.

Hiatt and Brock (1948, after unpublished data of J. Marr and O. Smith) stated that the scad, *Decapterus sanctaehelenae,* was most frequently encountered in the stomachs of dogtooth tunas in the Marshall Islands. Schultz in Schultz and collaborators (1953) reported that *D. muroadsi* and *Caesio xanthonotus* were regurgitated by *Gymnosarda nuda* (= *G. unicolor*) which were caught at Bikini.

Five of 17 specimens from the Marshall Islands taken during the survey had empty stomachs. The others contained fishes, five of which were identified as: *Naso brevirostris, N. vlamingii, Cirrhilabrus* sp., *Caesio* sp., *Pterocaesio* sp. The two prey specimens of *Naso* were large adults. The *N. vlamingii,* taken from the largest *G. unicolor,* measured 370 mm SL.

Labridae (Wrasses)

Cheilinus undulatus Rüppell (Figure 42): The giant humphead wrasse is one of the largest of bony fishes. It has been recorded to a length of 2.29 m and a weight of 190.5 kg (Marshall 1964). The hump on the forehead develops only on larger individuals. Two dark lines which extend posteriorly from the eye are useful in identifying juveniles and subadults of this species. It is usually found on outer reef slopes or in deep channels, but also occurs in lagoons. It is difficult to approach underwater. According to Bagnis et al. (1972) individual fish have a home cave to which they retreat when threatened and to which they retire at night. Randall (1958) reported this species as capable of being moderately to strongly toxic in Tahiti, where it is called "mara" (Randall 1972). It is one of nine species of fishes which are banned from sale in the Papeete market (Bagnis 1968).

Seven specimens, 515-995 mm SL, the largest weighing 34.5 kg, were procured at Enewetak for testing. The largest gave a reaction of 2 on feeding to mongooses; the others were 0.

Randall et al. (1978) reported on the food habits of the giant humphead wrasse based on the examination of 72 specimens from the Red Sea and islands of Oceania. The diet is highly varied, the dominant groups of food organisms being mollusks (gastropods a little more numerous than pelecypods), crustaceans (especially crabs), echinoids, and fishes. The hard parts of the invertebrates are crushed to fragments by the powerful pharyngeal dentition.

Coris aygula Lacepède (Figure 43): This is one of the two largest species of *Coris* (the other an undescribed endemic from Lord Howe Island). The largest collected, from the Red Sea, measured 465 mm SL and 583 mm TL. Adult males develop a gibbosity on the forehead similar to that of *Cheilinus undulatus,* but these two wrasses could hardly be confused; the *Coris* is more elongate (depth about 3.2 in SL) and has small scales (60-65 lateral line scales for *C. aygula,* compared with about 25 for *Cheilinus undulatus*); also, the lateral line of *Cheilinus* is interrupted.

Coris aygula has apparently not been reported as causing ciguatera but because of its large size and similar food habits it would seem to be at least as suspect as *C. gaimard* which is known to be poisonous at times. The latter is more colorful, displaying bright blue spots and a yellow caudal fin.

Five adults of *C. aygula,* 329-377 mm SL (0.9-1.9 kg), were obtained from Enewetak for testing. One of 368 mm SL (1.4 kg) produced a toxic reaction of 1 when its liver and viscera were fed to a mongoose; the others were nontoxic.

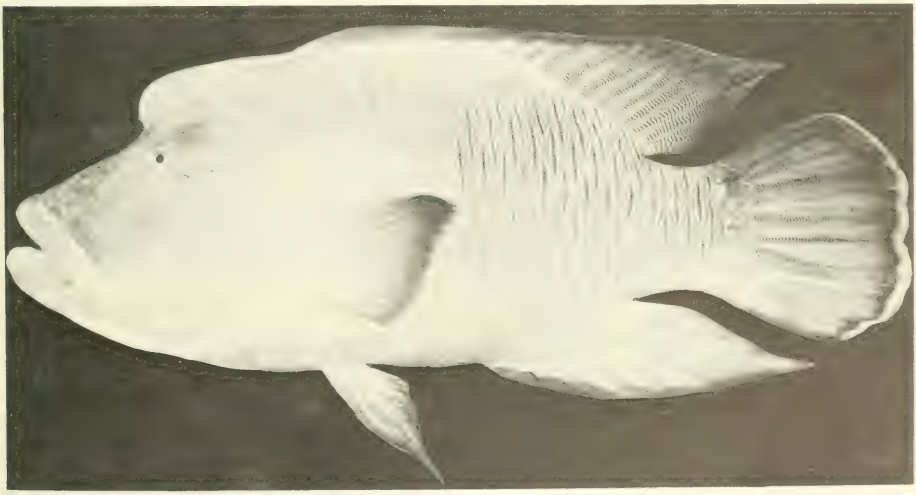


FIGURE 42.—*Cheilinus undulatus,* 915 mm SL, 25.8 kg, Enewetak, Marshall Islands.

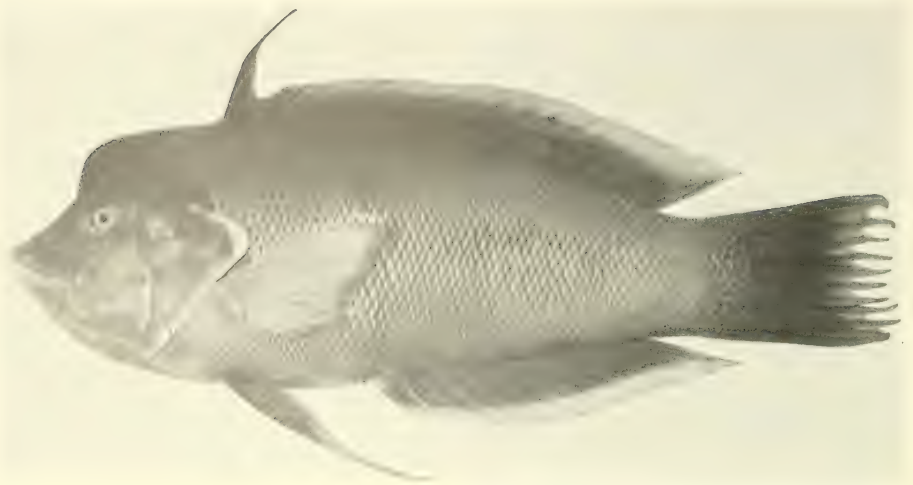


FIGURE 43.—*Coris aygula*, 380 mm SL, Marcus Island.

Al-Hussaini (1947) listed the food of the species as gastropods (*Turbo, Trochus*), *Dentalium,* and hermit crabs. Hiatt and Strasburg (1960) found the crushed remains of sand-dwelling pelecypods and gastropods in a single specimen (identified as *C. angulata*) from Enewetak.

Randall, G. J. Vermeij, and H. A. Rehder (manuscript in progress) will report in detail on the food habits of this wrasse. The principal food animals are gastropods, pelecypods, pagurid crabs, echinoids, and brachyuran crabs.

Epibulus insidiator (Pallas) (Figure 44): This unmistakable labrid, popularly known as the slingjaw wrasse because of its ability to enormously protrude its mouth, occurs from the Red Sea and east Africa to French Polynesia. Halstead (1967) listed nine references citing it as ciguatoxic.

Five specimens from Enewetak, 175-228 mm SL, 0.34-0.55 kg, were tested for toxicity. None caused any symptoms in the mongooses.

Hiatt and Strasburg (1960) collected one specimen from Enewetak and one from Bikini for food-habit study; both fish had eaten alpheid shrimps. They wrote, "This wrasse habitually feeds in ramose corals by extending its exceedingly protractile snout into the interstices to capture small alpheid shrimps and xanthid crabs living there."

For the present food-habit study 16 specimens, 183-240 mm SL, were collected from the Marshall Islands, Johnston Island, American Samoa, and the Society Islands. Two had empty stomachs; six had eaten only fishes and four only crabs. Other food items were shrimps, unidentified crustaceans, polychaetes, bryozoans, and unidentified eggs.

Scaridae (Parrotfishes)

Hipposcarus harid (Forsskål) (Figure 45): Smith (1956) created a new genus, *Hipposcarus,* for this species on the basis of the triangular patch of scales on the cheek with three or four rows behind, pointed snout, and minute nostrils. Although Schultz (1958, 1969) did not recognize this genus, it will be considered valid by Nelson and Randall.[9]

Smith (1959) described a Philippine form of this species as new, naming it *H. schultzi.* Schultz (1969) preferred to regard this form, for which he gave the range central and western Pacific Ocean, as a subspecies, *Hipposcarus harid longiceps* (Cuvier and Valenciennes).

Halstead (1967) has listed four references reporting the occasional toxicity of this parrotfish.

[9]G. J. Nelson, Department of Ichthyology, American Museum of Natural History, New York, and the author conferred in October 1977 on the generic limits of the Scaridae. Eventual publication is planned.

FIGURE 44.—*Epibulus insidiator,* 185 mm SL, Enewetak, Marshall Islands.

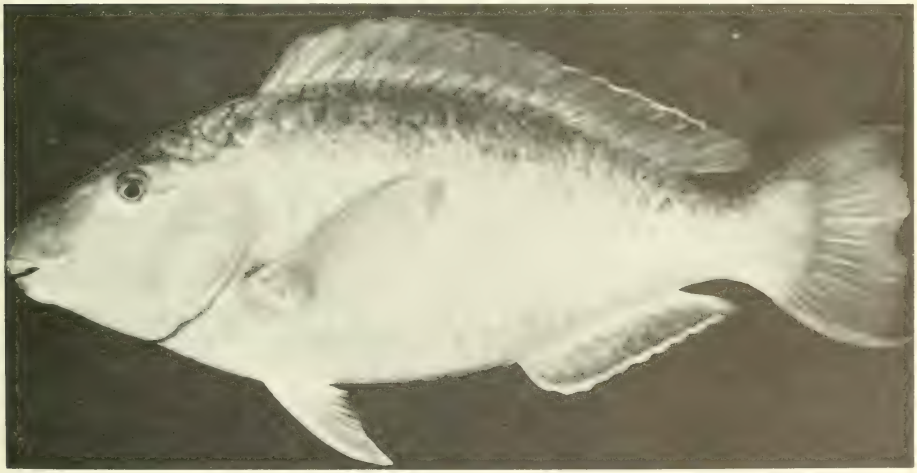


FIGURE 45.—*Hipposcarus harid,* 282 mm SL, Rangiroa, Tuamotu Archipelago.

Of four specimens, 340-412 mm SL, 1.3-1.8 kg, obtained at Enewetak, three were nontoxic, and one produced a reaction of 1.

Reporting on the stomach contents of *Cetoscarus bicolor, Scarus sordidus,* and seven unidentified species of *Scarus* in the Marshall Islands, Hiatt and Strasburg (1960) concluded that they fed mainly on live coral. This is contradictory to the investigation of scarid food habits by Wood-Jones (1910), Choat (1966), Randall (1967, 1974), Rosenblatt and Hobson (1969), and Hobson (1974). Randall (1974), however, presented evidence that the largest of the parrotfishes, *Bolbometopon muricatus,* feed heavily on living coral. Also Glynn et al. (1972) listed three scarids as coral predators off the Pacific coast of Panama.

Scarus gibbus Rüppell (Figure 46): The name *Scarus microrhinos* Bleeker has generally been used in the Pacific for this species (Schultz 1958), and it is under this name that its toxicity has been reported (Halstead 1967). Smith (1959) resurrected the name *Scarus gibbus* Rüppell for the Red Sea form of this species, though he still recognized *S. microrhinos*. Schultz (1969) placed four nominal species, including *S. microrhinos*, under the one name *S. gibbus*. The large males are readily distinguished by the near-vertical anterior profile of the head. Other useful characters for distinguishing the species are four median predorsal scales, three rows of scales on the cheek, and 16 or 17 pectoral rays.

Of 19 specimens, 326-414 mm SL, 1.05-2.8 kg, speared from Enewetak, only 1 of 410 mm (2.3 kg) was slightly toxic (mongoose reaction of 1).

Scarus rubroviolaceus Bleeker (Figure 47): This parrotfish was selected as the type-species of a new genus, *Scarops,* by Schultz (1958) principally on the basis of its having a single enlarged row of teeth on each upper pharyngeal bone. This genus, however, was not recognized by Rosenblatt and Hobson (1969). The primary phase of *S. rubroviolaceus* is reddish with small blackish spots and short streaks on the scales; the terminal male phase (the nominal *Pseudoscarus jordani* Jenkins and *Callyodon africanus* Smith were based on this form) is complexly colored, but mainly purplish on the anterior part of the body and abruptly green posterior to about the base of the seventh dorsal spine (this bicolored effect more evident in live than on freshly dead specimens); the head is mainly blue-green, shading to orange-yellow on the opercle, with transverse bands of turquoise and salmon on the lips and chin. There are generally 6 median predorsal scales, 3 rows of scales on the cheek, and 15 pectoral rays.

Like the other species of *Scarus*, *S. rubroviolaceus* is closely tied to coral reefs. It ranges from east Africa to the tropical eastern Pacific. Although this species has not been reported as poisonous, it would seem to have the same potentiality of causing ciguatera as other parrotfishes which may be toxic.

Three specimens, 355-370 mm SL, 1.4-1.6 kg, were obtained from Enewetak in order to test for possible toxicity. None were toxic.

Rosenblatt and Hobson (1969) wrote, "All of the eastern Pacific species of *Scarus* feed by scraping algae from the surface of rocks. We did not see evidence that they bit off pieces of coral..." *Scarus rubroviolaceus* is one of the four species they studied. Glynn et al. (1972), on the other hand, included *S. rubroviolaceus* among the three scarids they regarded as coral predators from observations off Panama.

Acanthuridae (Surgeonfishes)

Acanthurus xanthopterus Cuvier and Valenciennes (Figure 48): This is the largest member of

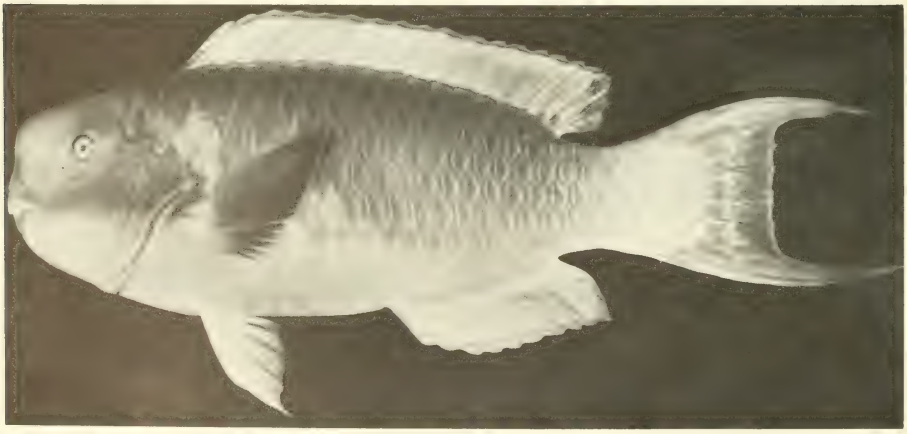


FIGURE 46.—*Scarus gibbus*, 417 mm SL, 2.8 kg, Tahiti, Society Islands.

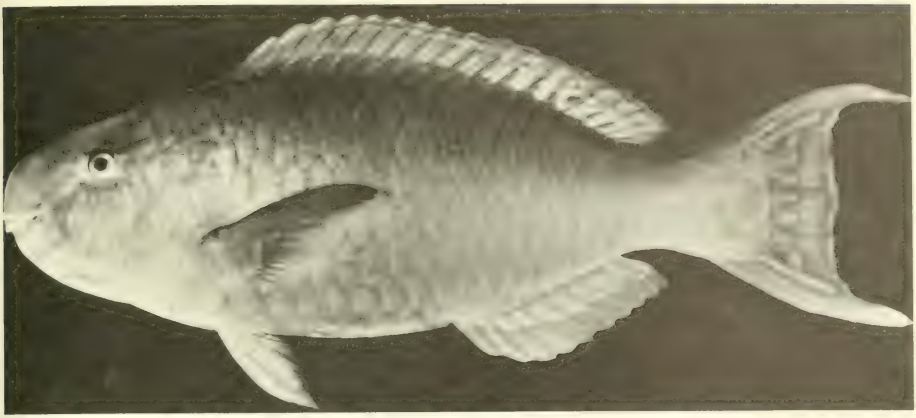


FIGURE 47.—*Scarus rubroviolaceus*, 355 mm SL, 1.35 kg, Enewetak, Marshall Islands.

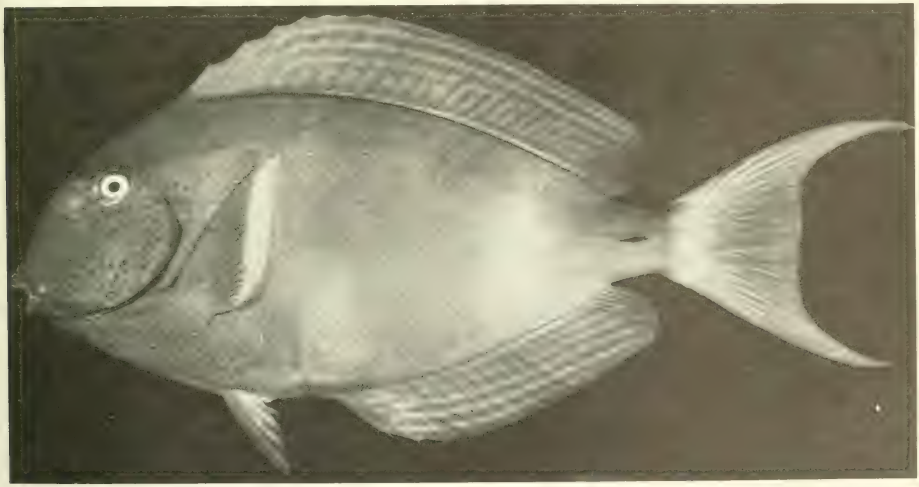


FIGURE 48.—*Acanthurus xanthopterus*, 400 mm SL, 2.3 kg, Enewetak, Marshall Islands.

the genus *Acanthurus*. It is one of a complex of species with a gizzardlike stomach. In the Marshall Islands it could only be confused with *A. mata*, also a large species. The outer third of the pectoral fins of *A. xanthopterus* are yellowish (fins uniform brown on *A. mata*), and there are about 4 lengthwise bands in the dorsal fin (about 8 in the fin of *A. mata*); there are fewer gill rakers (16-22 for *A. xanthopterus*, compared with 21-25 for *A. mata*). This species is distributed from east Africa to the eastern Pacific. It occurs more in lagoons and bays than exposed outer reef areas, and it ranges into deeper water than other *Acanthurus* in general. Also it ventures farther from the cover of coral reefs than other species. Schultz in Schultz and collaborators (1953) used the name *Acanthurus fuliginosus* Lesson for this fish, but there is no basis for equating it to Lesson's illustration and description, as explained by Randall (1956). The junior synonym *Teuthis crestonis* Jordan and

Starks was created for the species from Mexico.

Two specimens, 423 and 425 mm SL, 2.7 kg, were obtained from Enewetak for the assay of toxicity. Neither were toxic.

Hiatt and Strasburg (1960) examined the stomachs of four specimens from Enewetak, two of which were empty. The other two contained short filaments of algae with much sand, hydroid hydrocaulus, and wood splinters (probably from grazing on pilings). Jones (1968) classified *A. xanthopterus* as a grazer on diatoms and detritus in sand patches. That it will take animal food when the opportunity arises was aptly shown by Helfrich and Banner (1963) who used this species to induce ciguatera toxicity by feeding the poisonous flesh of *Lutjanus bohar*.

Ctenochaetus striatus (Quoy and Gaimard) (Figure 49): This surgeonfish is much the most common of the four species of the genus that occur in the Marshall Islands. It is, in fact, one of the most abundant reef fishes throughout the Indo-West Pacific region (though not Hawaii). The genus is named for its comblike teeth which are numerous, slender with expanded incurved tips, and flexible in the jaws. Randall (1955b) has differentiated *C. striatus* from the other species by having 5-7 denticulations on the expanded distal tips of the upper teeth, the highest average number of dorsal and anal soft rays (modally 29 dorsal rays and 26 or 27 anal rays), and a lunate caudal fin.

Bagnis et al. (1968) reported that surgeonfishes (particularly *C. striatus*) are responsible for 65% of the cases of ciguatera in Tahiti. There are three reasons for this: 1) the abundance of *C. striatus*, 2) its good-eating quality, and 3) the knowledge that the symptoms will be mild if ciguatera is incurred.

Bagnis (1968) documented the great variation in the symptoms of ciguatera in French Polynesia. He noted that digestive and neurologic symptoms predominated among those patients who had ingested surgeonfishes.

Yasumoto et al. (1971) determined that there are two principal toxins in *C. striatus*, one of which is fat soluble and chromatographically identical with ciguatoxin, and the other is water soluble. The latter was found only in the liver and gut contents. In a few specimens from Tahiti a different fat-soluble toxin and a different water-soluble toxin were detected.

In order to determine if more than one toxin is present in *C. striatus* in the Marshall Islands, 22 adult specimens were speared on lagoon reefs of

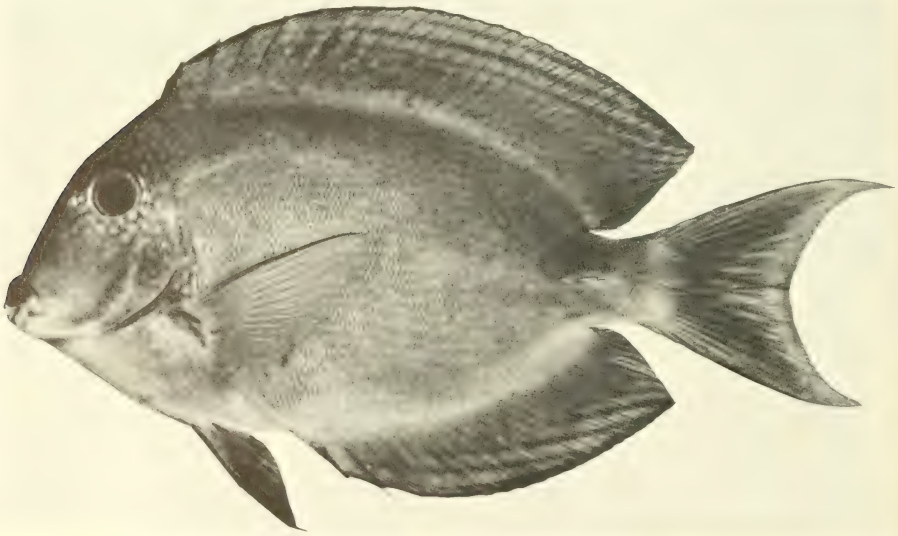


FIGURE 49.—*Ctenochaetus striatus*, 94 mm SL, Enewetak, Marshall Islands.

Enewetak and sent frozen to the Laboratory of Marine Biochemistry of the University of Tokyo. The specimens, which weighed from 130 to 230 g each, were pooled in groups of three (four for one group). The flesh and the viscera were separated for each group, and the gut contents of all groups were pooled. Fat-soluble and water-soluble fractions were prepared and injected intraperitoneally into mice at doses of 4,000, 2,000, and 1,000 μg/g. Two mice were used for each dose. If the mice were not killed by a dose of 4,000 μg/g within the observation period of 48 h, the preparation was regarded as nontoxic. If they were killed by a dose of 1,000 μg/g, it was classified as strongly toxic, at 2,000 μg/g moderately toxic, and at 4,000 μg/g weakly toxic. The results were reported in a letter by the late Yoshiro Hashimoto, then the Director of the Laboratory. None of the preparations were strongly toxic. All the preparations from the flesh were nontoxic. Four of the seven fat-soluble preparations of the viscera were moderately toxic, one was weakly toxic, and one nontoxic. Five of the seven water-soluble fractions from the viscera were weakly toxic and the remaining two nontoxic. Both the fat-soluble and the water-soluble preparations of the pooled gut contents were moderately toxic.

The food habits and mode of feeding of *C. strigosus* from the Hawaiian Islands were investigated by Randall (1955b); underwater observations of *C. striatus* indicate that its feeding is essentially the same. These fishes are detritus feeders. From a near-vertical position (if the bottom is horizontal) about 15 mm above the substratum, the fish move abruptly downward with mouth open. The lips and teeth scrape over the surface at the same time that suction is initiated. The soft detrital material and fine inorganic sediment are ingested. If coarse particles of sand are picked up, they are forcefully ejected. The stomach contents of seven adults of *C. strigosus* from Hawaii consisted of inorganic sediment (up to 90% by volume); fragments of red, green, and blue-green algae; diatoms; and unidentified soft organic material. In an aquarium experiment *C. strigosus* was unable to feed on an intact thallus of the filamentous alga *Polysiphonia* sp. When the same algae was finely fragmented and placed on the bottom, it was readily consumed.

Balistidae (Triggerfishes)

Pseudobalistes flavimarginatus (Rüppell) (Figure 50): This is one of three large species of triggerfishes that occur in the Marshall Islands. It may be distinguished from other balistids by the following characters collectively: the second dorsal and anal fins elevated anteriorly, five or six rows of spines on the caudal peduncle, no scales on the cheek (of adults), caudal fin of adults emarginate, and yellowish margins on the median fins. Woods in Schultz and collaborators (1966) failed to list this species from the Marshall Islands, but the color plate in Hiyama (1943, pl. 22, fig. 61) and the study of Hiatt and Strasburg (1960) clearly indicate its presence there. Hiatt and Strasburg stated that it is solitary, uncommon, and occurs on lagoon and interisland reefs in quiet water of 10-30 ft (3.1-9.1 m) deep. Although Hiyama wrote that this fish was not regarded as poisonous in the Marshalls, other records (Halstead 1967) demonstrate its capacity for causing ciguatera. It is one of the nine species of fishes forbidden to be sold in the fish market in Papeete, Tahiti (Bagnis 1968).

Two specimens, 465 and 535 mm SL, weight not taken, were collected in Bikini. Neither was poisonous.

Clark and Gohar (1953) reported pieces of branched coral (*Stylophora*) 2-3 cm long in the stomach of a specimen 440 mm SL from the Red Sea. Hiatt and Strasburg (1960) examined two stomachs from the Marshall Islands. They found the crustacean *Lydia annulipes* and isopods, crushed gastropods including *Oliva* sp., foraminifera, and colonial tunicate fragments.

The stomach and gut contents of only two specimens were obtained for the present study. One of 254 mm SL from the Red Sea was empty. The second of 390 mm SL from Tahiti had eaten *Diadema*.

Balistoides viridescens (Bloch and Schneider) (Figure 51): This is another large triggerfish for which there have been a few records of toxicity. It shares the elevated anterior part of the second dorsal and anal fins and the rows of spines on the caudal peduncle with *P. flavimarginatus*, but is differentiated by having its cheek totally scaled and its caudal fin rounded to slightly double emarginate as an adult; also the margins of its median fins are broadly blackish. It ranges from the Red Sea to eastern Oceania. It occurs in both lagoons and outer reef slopes. Like other triggerfishes, it has a favorite hiding place in the reef into which it wedges itself when threatened.

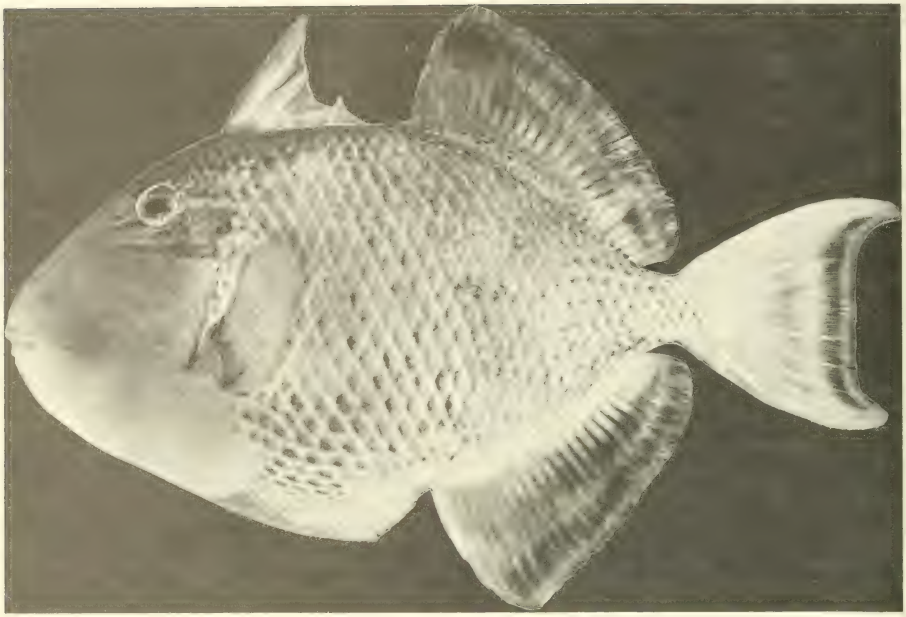


FIGURE 50.—*Pseudobalistes flavimarginatus*, 265 mm SL, Palmyra, Line Islands.

A single specimen, 456 mm SL, 4.5 kg, from Enewetak was nontoxic.

The stomach and gut contents of four specimens, 278-525 mm SL, from the Society Islands and the Red Sea were examined. Echinoids, including *Diadema*, *Echinometra*, and spatangoids, were the main items of diet, but pelecypods, crabs, polychaete tube worms, gastropods, chitons, foraminifera, and algae and detritus were also present.

DISCUSSION AND SUMMARY

As mentioned in introductory remarks, the initial testing for level of ciguatera at both Enewetak and Bikini revealed only an occasional toxic fish among the species responsible for most cases of this type of poisoning in the Pacific. As expected, the toxic individuals were invariably adults of moderate to large size for the species. A decision was then made to concentrate the fishing effort on the larger individuals of the species most often implicated in ciguatera. These dangerous species are, in general, not common. They are at or near the peak of the well-known "pyramid of numbers," i.e., the reduction in number of individuals one encounters analyzing the populations in successive steps up the food chain. Consequently, much more effort was expended in catching not only these fishes but just the larger individuals of these species. Also, it is for this reason that some relatively common species such as *Lutjanus fulvus* and *Adioryx spinifer* are represented by few individuals in this report and others such as the smaller species of groupers of the genera *Epinephelus* and *Cephalopholis* were not collected. In highly toxic sectors these species can be poisonous, though even there the incidence is low.

A total of 551 specimens of 48 species were tested from Enewetak and 256 specimens of 23 species from Bikini. In addition, 12 adult specimens of *Lutjanus bohar* from Rongelap were tested, one of which was toxic at the 5 level. The results of the testing of fishes from Enewetak are summarized in Table 1, and for Bikini in Table 2; 37.3% of the fishes from Enewetak gave a positive reaction for ciguatoxin, and 19.7% of those from Bikini.

FIGURE 51.—*Balistoides viridescens*, 456 mm SL, 4.5 kg, Tetiaroa, Society Islands.

It must be emphasized that liver and viscera of the suspect fishes were used in the mongoose feeding tests (except for sharks) and not flesh. Because of the much higher level of ciguatoxin in the internal organs than in muscle tissue, low-level toxicity (indicated by mongoose reactions of 1 or 2) from liver and viscera would probably not result in a detectable level of toxin if flesh from these fishes had been used in the tests. When the percentage of toxicity is computed for the reactions 3-5 (it is this level at which a human eating the flesh of these species might be expected to fall ill with ciguatera), the percentage of toxic fishes drops to 16.2 for Enewetak and 1.4 for Bikini.

When one considers the effort directed almost entirely to the worst offenders in ciguatera, the level of toxicity at Enewetak must be regarded as relatively low and that of Bikini decidedly so. Most of these fishes are avoided as adults by islanders in Oceania regardless of the area of capture. Therefore it is concluded that the returning residents to Enewetak and Bikini need not fear at this time any unexpected threat of ciguatera at their atolls.

Only eight species of fishes produced reactions of 4 or 5 in the test animals; that is, severe illness or death: *Lycodontis javanicus*, *Cephalopholis argus*, *Epinephelus hoedtii*, *E. microdon*, *Plectropomus leopardus*, *Aprion virescens*, *Lutjanus bohar*, and *Lethrinus kallopterus*. Had more specimens of *Sphyraena barracuda*, *Caranx ignobilis*, and *Cheilinus undulatus*, particularly of large size (none of the specimens taken during this survey approached the maximum size), been collected, then they may be expected to be included in the above list (in view of their reputations for causing ciguatera in other areas).

The moray *Lycodontis javanicus* was clearly the most toxic of all the species tested, with all individuals producing a reaction of 2 or more in mongooses and one-third of them the lethal 5.

Randall (1958) analyzed the kinds of fishes which have caused ciguatera in terms of habitat, mode of life, and food habits. These species are shore fishes associated with reefs. Usually they are bottom-dwelling generally in < 60 m, but they may be semipelagic open-water forms that range into the reef habitat to feed. They may be carnivorous or they may feed on benthic algae or detritus. Of the carnivores, those that prey heavily on reef fishes are the most prone to be poisonous,

whereas those that eat mainly benthic crustaceans the least. Fishes that feed wholly or primarily on plankton are not apt to be toxic. Some mollusk and echinoid feeders may cause severe cases of ciguatera. The level of toxicity among benthic herbivores and detritus feeders is consistently low.

The food-habit studies of this survey support these generalizations. Seven of the eight most toxic species are piscivorous. The one other, *Lethrinus kallopterus*, appears to feed mainly on echinoids and mollusks. No specimens of *Lutjanus fulvus*, *Epinephelus socialis*, and *Adioryx spinifer* were found to be toxic (although relatively few specimens were collected); these feed more on crustaceans than fishes. Among the herbivores tested, only two individuals of *Scarus* and one of *Kyphosus* gave a reaction of 1. A water-soluble toxin as well as ciguatoxin were found in the detritus-feeding surgeonfish *Ctenochaetus striatus*, but in small amounts.

The relatively low level of ciguatoxin in sharks is surprising. Because they feed heavily on fishes and are believed to be long-lived, one might expect them to be as ciguatoxic as the larger moray eels. The tropical species of sharks are not as widely eaten as bony fishes. If they were, no doubt more cases of ciguatera would be attributed to them. The species of *Carcharhinus* appear to prey to a significant degree on pelagic fishes, and when they do feed on reef-dwelling species, they seem to take many plankton-feeding forms. This may in part explain their apparent relatively low level of ciguatoxin. Still another possibility is that sharks may not accumulate as much ciguatoxin in their tissues as bony fishes.

Because ciguatera can be highly localized to certain reefs or even sectors of reefs, the fish collecting was carried out at many different locations at the atolls. No one area was detected as having a notably higher level of toxicity.

Many of the most dangerous ciguatoxic species are roving predators. Examples are the barracudas, jacks, dogtooth tuna, emperors, and, to a lesser extent, the snappers. They can be caught at a different area from which they acquired most of their toxicity. The strong localization of ciguatera occurs more where the level of toxicity is high and the smaller more resident species are poisonous. Our fishing has not been sufficiently extensive to demonstrate minor differences in the incidence of ciguatera with locality.

At Enewetak most of the fishing was undertaken on the southern part of the atoll, particularly in the vicinity of Enewetak Island, the largest of the atoll. This island had the largest population of Marshallese people before they were evacuated from the atoll, and it is expected that it will have the largest number when all have been repatriated. Also it is in this area that most of the long-term disturbances of the marine environment, such as the dumping of unwanted material, have taken place. It is fortunate that ciguatera, though more in evidence at Enewetak than at Bikini, is not a major problem as might have been predicted from the impact of western man on the atoll.

ACKNOWLEDGMENTS

The author and associates acknowledge with gratitude the support of the U.S. Energy Research and Development Administration through contract E(26-1)-641 with the University of Hawaii and Bernice P. Bishop Museum, Honolulu.

The following individuals participated in the fishing program in the Marshall Islands: Gerald S. Akiyama, Bruce A. Carlson, the late David Erlenkotter, Glen H. Fredholm, James W. Fry, Gregory Gahagan, Gerald Gulden, Walter C. Gutjahr, Guy S. Haywood, George MacGuire, Oliver K. McCausland, Rhett M. McNair, Robert F. Meyers, Takeo Okamura, John E. Randall, Robert P. H. Rutherford, Arnold Y. Suzumoto, and Gordon W. Tribble. In addition, Phillip B. Lamberson, formerly of the Mid-Pacific Marine Laboratory, Harry J. Miller and Russell E. Miller, former resident personnel of the atoll, assisted in the collecting at Enewetak.

The testing of the toxicity was carried out by James Murphy and Lambert Yamashita at the Hawaii Institute of Marine Biology of the University of Hawaii, under the direction of A. H. Banner, except for the last sampling in May 1978 for which an initial screening was made by Yoshitsugi Hokama of the Department of Pathology, University of Hawaii, by radioimmunoassay (Hokama et al. 1977). The higher reactions were then confirmed by mongoose feeding at the Bernice P. Bishop Museum by Arnold Y. Suzumoto.

A. H. Banner and Helen A. Randall provided helpful suggestions and reviewed the manuscript.

LITERATURE CITED

ADACHI, R., AND Y. FUKUYO.
1979. The thecal structure of a marine toxic dinoflagellate

Gambierdiscus toxicus gen. et sp. nov. collected in a ciguatera-endemic area. Bull. Jpn. Soc. Sci. Fish. 45:67-71.

AL-HUSSAINI, A. H.
1947. The feeding habits and the morphology of the alimentary tract of some teleosts living in the neighbourhood of the Marine Biological Station, Ghardaqa, Red Sea. Publ. Mar. Biol. Stn. Ghardaqa (Red Sea) 5:1-61.

BAGNIS, R.
1968. Clinical aspects of ciguatera (fish poisoning) in French Polynesia. Hawaii Med. J. 28:25-28.
1969. Naissance et développement d'une flambée de ciguatera dans un atoll des Tuamotu. Rev. Corps Santé 10(6):783-795.

BAGNIS, R., J. BENNETT, V. JOUTAIN, AND F. NANAI.
1968. Ciguatera in Tahiti: an endemic disease. South Pac. Comm. Sem. Ichthyosarcotoxism, Fr. Polynesia, 15 p.

BAGNIS, R., P. MAZELLIER, J. BENNETT, AND E. CHRISTIAN.
1972. Poissons de Polynésie. Les Editions du Pacifique, Papeete, 368 p.

BANNER, A. H.
1965. Ciguatera fish poisoning: a symposium. Ciguatera in the Pacific. Hawaii Med. J. 24:353-361.

BANNER, A. H., AND P. HELFRICH.
1964. The distribution of ciguatera in the tropical Pacific. Hawaii Mar. Lab. Tech. Rep. 3, 48 p.

BANNER, A. H., P. HELFRICH, AND T. PIYAKARNCHANA.
1966. Retention of ciguatera toxin by the red snapper, *Lutjanus bohar*. Copeia 1966:297-301.

BANNER, A. H., P. J. SCHEUER, S. SASAKI, P. HELFRICH, AND C. B. ALENDER.
1960. Observations on ciguatera-type toxin in fish. Ann. N.Y. Acad. Sci. 90:770-787.

BARTSCH, A. F., R. H. DRACHMAN, AND E. F. MCFARREN.
1959. Report of a survey of the fish poisoning problem in the Marshall Islands. U.S. Dep. Health, Educ., Welfare, Public Health Serv., 117 p.

BASS, A. J., J. D. D'AUBREY, AND N. KISTNASAMY.
1973. Sharks of the east coast of southern Africa. I. The genus *Carcharhinus* (Carcharhinidae). Oceanogr. Res. Inst. (Durban) Invest. Rep. 33, 168 p.
1975a. Sharks of the east coast of southern Africa. III. The families Carcharhinidae (excluding *Mustelus* and *Carcharhinus*) and Sphyrnidae. Oceanogr. Res. Inst. (Durban) Invest. Rep. 38, 100 p.
1975b. Sharks of the east coast of southern Africa. IV. The families Odontaspididae, Scapanorhynchidae, Isuridae, Cetorhinidae, Alopiidae, Orectolobidae and Rhiniodontidae. Oceanogr. Res. Inst. (Durban) Invest. Rep. 39, 102 p.

BECKE, L.
1901. Poisonous fish of the Pacific Islands. *In* L. Becke, Yorke the adventurer, p. 246-254, J. B. Lippincott Col., Lond.

BELOTTE, J.
1955. Les Poissons "empoisonnés" du lagon Tahitien. Méd. Trop. 15:232-236.

BIGELOW, H. B., AND W. C. SCHROEDER.
1948. Sharks. *In* A. E. Parr (editor), Fishes of the western North Atlantic, Part one, p. 59-546. Mem. Sears Found. Mar. Res., Yale Univ. 1.

BOULENGER, G. A.
1895. Catalogue of the perciform fishes in the British Museum. 2d ed., Vol. 1. Br. Mus. (Nat. Hist.), Lond., 394 p.

BROCK, R. E.
1972. A contribution to the biology of *Gymnothorax javanicus* (Bleeker). M.S. Thesis, Univ. Hawaii, 121 p.

BROCK, V. E., R. S. JONES, AND P. HELFRICH.
1965. An ecological reconnaissance of Johnston Island and the effects of dredging. Hawaii Mar. Lab. Tech. Rep. 5, 90 p.

CHOAT, J. H.
1966. Parrot fish. Aust. Nat. Hist. 15:265-268.

CLARK, E., AND H. A. F. GOHAR.
1953. The fishes of the Red Sea: Order Plectognathi. Publ. Mar. Biol. Stn. Al Ghardaqa (Red Sea) 8, 80 p.

CLARK, E., AND K. VON SCHMIDT.
1965. Sharks of the central Gulf coast of Florida. Bull. Mar. Sci. 15:13-83.

COMPAGNO, L. J. V.
1973. *Gogolia filewoodi*, a new genus and species of shark from New Guinea (Carcharhiniformes: Triakidae), with a redefinition of the family Triakidae and a key to triakid genera. Proc. Calif. Acad. Sci., Ser. 4, 39:383-410.

COOPER, M. J.
1964. Ciguatera and other marine poisoning in the Gilbert Islands. Pac. Sci. 18:411-440.

DE SYLVA, D. P.
1963. Systematics and life history of the great barracuda *Sphyraena barracuda* (Walbaum). Stud. Trop. Oceanogr. (Miami) 1, 179 p.
1973. Barracudas (Pisces: Sphyraenidae) of the Indian Ocean and adjacent seas - a preliminary review of their systematics and ecology. J. Mar. Biol. Assoc. India 15:74-94.

FOURMANOIR, P.
1961. Requins de la cote ouest de Madagascar. Mém. Inst. Sci. Madagascar, sér. F, 4:1-81.

GARRICK, J. A. F.
1967. A broad overview of *Carcharhinus* species, their systematics and distribution. *In* P. W. Gilbert, R. F. Mathewson, and D. R. Rall (editors), Sharks, skates, and rays, p. 85-91. Johns Hopkins Press, Baltimore.
In press. Sharks of the genus *Carcharhinus*. U.S. Dep. Commer., NOAA Tech. Rep. NMFS Circ.

GLYNN, P. W., R. H. STEWART, AND J. E. MCCOSKER.
1972. Pacific coral reefs of Panamá: structure, distribution and predators. Geol. Rundsch. 61:483-519.

GOHAR, H. A. F., AND F. M. MAZHAR.
1964. The elasmobranchs of the north-western Red Sea. Publ. Mar. Biol. Stn. Al-Ghardaqa (Red Sea) 13:1-144.

HALSTEAD, B. W.
1967. Poisonous and venomous marine animals of the world, Vol. 2. U.S. Gov. Print. Off., Wash., D.C., 1070 p.

HALSTEAD, B. W., AND W. M. LIVELY, JR.
1954. Poisonous fishes and ichthyosarcotoxism. Their relationship to the Armed Forces. U.S. Armed Forces Med. J. 5:157-175.

HALSTEAD, B. W., AND D. W. SCHALL.
1958. A report on the poisonous fishes of the Line Islands. Acta Trop. 15:193-233.

HARMELIN-VIVIEN, M. L., AND C. BOUCHON.
1976. Feeding behavior of some carnivorous fishes (Serranidae and Scorpaenidae) from Tuléar (Madagascar). Mar. Biol. (Berl.) 37:329-340.

HELFRICH, P., AND P. A. ALLEN.
1975. Observations on the spawning of mullet, *Crenimugil*

crenilabis (Förskal), at Enewetak, Marshall Islands. Micronesica 11:219-225.

HELFRICH, P., AND A. H. BANNER.
1963. Experimental induction of ciguatera toxicity in fish through diet. Nature (Lond.) 197:1025-1026.
1968. Ciguateric fish poisoning. II. General patterns of development in the Pacific. Occas. Pap. Bernice P. Bishop Mus. 23:371-382.

HELFRICH, P., T. PIYAKARNCHANA, AND P. S. MILES.
1968. Ciguatera fish poisoning. 1. The ecology of ciguateric reef fishes in the Line Islands. Occas. Pap. Bernice P. Bishop Mus. 23:305-369.

HIATT, R. W., AND V. E. BROCK.
1948. On the herding of prey and the schooling of the black skipjack, *Euthynnus yaito* Kishinouye. Pac. Sci. 2:297-298.

HIATT, R. W., AND D. W. STRASBURG.
1960. Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. Ecol. Monogr. 30:65-127.

HISHIKARI, J.
1921. On poisonous fishes in South Sea Islands. [In Jpn.] Nippon Beseibut. Zasshi 16:1533-1543.

HIYAMA, Y.
1943. Report of an investigation of poisonous fishes of South Seas. [In Jpn.] Nissan Fish. Exp. Stn. Odawara Br., 137 p. (Translated by W. G. Van Campen, 1950, Poisonous fishes of the South Seas, p. 1-188. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 25.)

HOBSON, E. S.
1974. Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. Fish. Bull., U.S. 72:915-1031.

HOKAMA, Y., A. H. BANNER, AND D. B. BOYLAN.
1977. A radioimmunoassay for the detection of ciguatoxin. Toxicon 15:317-325.

HYDROGRAPHIC OFFICE, U.S. NAVY.
1945. Sailing directions for the Pacific Islands. Vol. I. Western groups, ed. 5. H. O. Publ. 165, 775 p.

JOHNSON, R. H., AND D. R. NELSON.
1973. Agonistic display in the gray reef shark, *Carcharhinus menisorrah*, and its relationship to attacks on man. Copeia 1973:76-84.

JONES, R. S.
1968. Ecological relationships in Hawaiian and Johnston Island Acanthuridae (surgeonfishes). Micronesica 4:309-361.

KATAYAMA, M.
1960. Fauna Japonica. Serranidae (Pisces). Tokyo News Serv., Tokyo, 189 p.

KATO, S., S. SPRINGER, AND M. H. WAGNER.
1967. Field guide to eastern Pacific and Hawaiian sharks. U.S. Fish Wildl. Serv., Circ. 271, 47 p.

KHLENTZOS, C. T.
1950. Seventeen cases of poisoning due to ingestion of an eel, *Gymnothorax flavimarginatus*. Am. J. Trop. Med. 30:785-793.

MARSHALL, T. C.
1964. Fishes of the Great Barrier Reef and coast waters of Queensland. Angus and Robertson, Sydney, 566 p.

MASUDA, H., C. ARAGA, AND T. YOSHINO.
1975. Coastal fishes of Southern Japan. Tokai Univ. Press, Tokyo, 379 p.

MATSUO, R.
1934. Investigation of the poisonous fishes of Jaluit Island. [In Jpn.] Nanyo Gunto Chihobyo Chosa Ronbunshu 2:309-326.

RANDALL, J. E.
1955a. Fishes of the Gilbert Islands. Atoll Res. Bull. 47, 243 p.
1955b. A revision of the surgeon fish genus *Ctenochaetus*, family Acanthuridae, with descriptions of five new species. Zoologica (N.Y.) 40:149-166.
1956. A revision of the surgeon fish genus *Acanthurus*. Pac. Sci. 10:159-235.
1958. A review of ciguatera, tropical fish poisoning, with a tentative explanation of its cause. Bull. Mar. Sci. Gulf Caribb. 8:236-267.
1963. A fatal attack by the shark *Carcharhinus galapagensis* at St. Thomas, Virgin Islands. Caribb. J. Sci. 3(4):201-205.
1964. Notes on the groupers of Tahiti, with description of a new serranid fish genus. Pac. Sci. 18:281-296.
1967. Food habits of reef fishes of the West Indies. Stud. Trop. Oceanogr. (Miami) 5:665-847.
1969. How dangerous is the moray eel? Aust. Nat. Hist. 16(6):177-182.
1972. Tahitian fish names and a preliminary checklist of the fishes of the Society Islands. Occas. Pap. Bernice P. Bishop Mus. 24:167-214.
1974. The effect of fishes on coral reefs. Proc. 2d Int. Coral Reef. Symp. 1:159-166.
1977. Contribution to the biology of the whitetip reef shark (*Triaenodon obesus*). Pac. Sci. 31:143-164.

RANDALL, J. E., AND V. E. BROCK.
1960. Observations on the ecology of epinepheline and lutjanid fishes of the Society Islands, with emphasis on food habits. Trans. Am. Fish. Soc. 89:9-16.

RANDALL, J. E., S. M. HEAD, AND A. P. L. SANDERS.
1978. Food habits of the giant humphead wrasse, *Cheilinus undulatus* (Labridae). Environ. Biol. Fish. 3(2):235-238.

RANDALL, J. E., AND G. S. HELFMAN.
1973. Attacks on humans by the blacktip reef shark (*Carcharhinus melanopterus*). Pac. Sci. 27:226-238.

ROBSON, R. W. (editor).
1959. Pacific Islands Year Book, 8th ed. Pac. Publ., Sydney, 479 p.

ROSENBLATT, R. H., AND E. S. HOBSON.
1969. Parrotfishes (Scaridae) of the eastern Pacific, with a generic rearrangement of the Scaridae. Copeia 1969:434-453.

ROSS, S. G.
1947. Preliminary report on fish poisoning at Fanning Island (Central Pacific). Med. J. Aust. 34(2):617-621.

SATO, T.
1978. A synopsis of the sparoid fish genus *Lethrinus*, with the description of a new species. Univ. Mus., Univ. Tokyo, Bull. 15, 70 p.

SCHULTZ, L. P.
1949. At grips with a giant moray eel. Nat. Hist. 58:42-43.
1958. Review of the parrotfishes family Scaridae. U.S. Natl. Mus. Bull. 214, 143 p.
1969. The taxonomic status of the controversial genera and species of parrotfishes with a descriptive list (family Scaridae). Smithson. Contrib. Zool. 17, 49 p.

SCHULTZ, L. P., AND COLLABORATORS.
1953-66. Fishes of the Marshall and Marianas Islands. U.S. Natl. Mus. Bull. 202, 3 vol.

SMITH, J. L. B.
1956. The parrotfishes of the family Callyodontidae of the

western Indian Ocean. Rhodes Univ., Grahamstown, Ichthyol. Bull. 1:1-23.

1959. The identity of *Scarus gibbus* Ruppell, 1828 and of other parrotfishes of the family Callyodontidae from the Red Sea and the western Indian Ocean. Rhodes Univ., Grahamstown, Ichthyol. Bull. 16:265-282.

SMITH, J. L. B., AND M. M. SMITH.

1963. The fishes of Seychelles. Dep. Ichthyol., Rhodes Univ., Grahamstown, 215 p.

STEINBACH, E.

1895. Bericht über die Gesundheitsverhältnisse der Eingeborenen der Marshallinseln im Jahre 1893/94 und Bemerhung über Fischgift. Mitt. Forschung. Gelehrt dtsch. Schutzgeb. 8(2):157-171.

STEPHENS, W. M.

1963. Stay away from the moray. Sea Front. 9:152-159.

TALBOT, F. H.

1960. Notes on the biology of the Lutjanidae (Pisces) of the East African coast, with special reference to *L. bohar* (Forskal). Ann. S. Afr. Mus. 45:549-573.

TAYLOR, F. J. R.

1979. A description of the benthic dinoflagellate associated with ciguatoxin, including observations on Hawaiian material. *In* D. L. Taylor and H. H. Seliger (editors), Toxic dinoglagellate blooms, p. 71-76. Elsevier, North Holland.

WASS, R. C.

1971. A comparative study of the life history, distribution, and ecology of the sandbar shark and the gray reef shark in Hawaii. Ph.D. Thesis, Univ. Hawaii, 219 p.

WHEELER, J. F. G., AND F. D. OMMANNEY.

1953. Report on the Mauritius-Seychelles Fisheries Survey 1948-1949. Colon. Off. Fish. Publ. 1(3):1-145.

WOOD-JONES, F.

1910. Coral and atolls. Reeve and Co., Lond., 392 p.

YASUMOTO, T., Y. HASHIMOTO, R. BAGNIS, J. E. RANDALL, AND A. H. BANNER.

1971. Toxicity of the surgeonfishes. Bull. Jpn. Soc. Sci. Fish. 37:724-734.

YASUMOTO, T., I. NAKAJIMA, R. BAGNIS, AND R. ADACHI.

1977. Finding of a dinoflagellate as a likely culprit of ciguatera. Bull. Jpn. Soc. Sci. Fish. 43:1021-1026.

YASUMOTO, T., I. NAKAJIMA, Y. OSHIMA, AND R. BAGNIS.

1979. A new toxic dinoflagellate found in association with ciguatera. *In* D. L. Taylor and H. H. Seliger (editors), Toxic dinoflagellate blooms, p. 65-70. Elsevier, North Holland.

YUDKIN, W. H.

1944. Tetrodon poisoning. Bull. Bingham Oceanogr. Collect. Yale Univ. 9(1), 18 p.

CALLINECTES (DECAPODA: PORTUNIDAE) LARVAE IN THE MIDDLE ATLANTIC BIGHT, 1975-77[1]

PETER O. SMYTH[2]

ABSTRACT

Distribution of *Callinectes* larvae in surface (neuston) and subsurface shelf waters in the Middle Atlantic Bight was determined from quarterly zooplankton collections taken during a 2-year study. Observations confirmed the presence in offshore waters of a large larval pool from which recruitment may take place. Larvae were predominantly late zoeae and megalope, with peak abundances in late summer collections reaching 16,000 per 100 m^3 in neuston collections. During summer, crab larvae were distributed across the shelf with the majority at 10-80 km offshore. Abundances were significantly greater in neuston than subsurface zooplankton collections and generally greater in neuston collections taken at night. Water temperature and distance from shore were factors most closely correlated with abundance of larvae in the neuston. Megalopae of *Callinectes* were present at outer shelf stations in winter and spring and together with megalopae of *Portunus* and other forms were of southern origin. Based on experimentally determined temperature-salinity preferences reported in the literature for *Callinectes* larvae, metamorphosis may be delayed in cooler offshore waters, thus increasing chances of long-range transport.

The community of organisms of the surface layer (the neuston[3]) has received increasing attention in terms of sampling problems and possible ecological significance. Zaitsev (1970) described the neuston as consisting chiefly of early developmental stages of fishes and invertebrates. Berkowitz (1976) and Morris (1975), however, found oceanic neuston faunistically impoverished in comparison with zooplankton of the immediate subsurface. Few studies of the neuston of shelf and shallow waters exist; preliminary indications are that the zooplankton of the surface waters of the continental shelf are at least quantitatively enriched (Grant[4]).

Callinectes, euryhaline members of the predominantly marine Portunidae, spawn along the shore of open oceans and in mouths of inlets and estuaries. Larval development occurs in shelf waters, with probable return inshore by megalopae and juveniles (Williams 1965, 1971, 1974; Costlow 1967; Tagatz 1968). *Callinectes* megalopae have been reported offshore in shelf waters (Nichols and Keney 1963; Dudley and Judy 1971); retention in shelf waters and subsequent transport of megalopae have been proposed as mechanisms in dispersal, widespread distribution, and maintenance of genetic continuity in the species (Costlow 1967; Williams 1971, 1974; Cole and Morgan 1978).

Callinectes larvae, at least zoeae, have surface affinities (Tagatz 1968; Dudley and Judy 1971; Sandifer 1972), but megalopae have generally been less numerous in collections than zoeae and limited to bottom samples (Tagatz 1968; Sandifer 1972; Goy 1976). Williams (1971), however, reported *Callinectes* megalopae to be active in estuarine surface waters at night.

With the widespread distribution and known abundance of *Callinectes* adults and the accepted migratory sequence of developmental stages (inshore-offshore-inshore), the reported abundance of late stage larvae is surprisingly low. Furthermore, the existence in shelf waters of a *Callinectes* larval pool from which recruitment to estuaries may occur is based on relatively few studies and limited sampling.

This paper reports the identification, distribution, and abundance of *Callinectes* larvae in neus-

[1]Contribution No. 952 from the Virginia Institute of Marine Science. From part of a dissertation to be submitted in partial fulfillment of requirements for the degree of Doctor of Philosophy, College of William and Mary.

[2]Virginia Institute of Marine Science and School of Marine Science, the College of William and Mary, Gloucester Point, VA 23062.

[3]Neuston has generally been defined operationally as the community of organisms sampled by gear specifically designed to sample the surface layer. The term is used in that sense in this paper. For a review of numerous terms associated with the surface layers, see Banse (1975).

[4]Grant, G. C. 1977. Middle Atlantic Bight zooplankton: seasonal bongo and neuston collections along a transect off southern New Jersey. Spec. Rep. Appl. Mar. Sci. Ocean Eng., Va. Inst. Mar. Sci. 173, 138 p.

Manuscript accepted November 1979.
FISHERY BULLETIN: VOL. 78, NO. 2, 1980.

ton and subsurface water column collections from shelf waters in the Middle Atlantic Bight. My objectives specifically were to: 1) determine whether a reservoir of *Callinectes* larvae, particularly megalopae, exists in shelf waters; 2) determine abundance relationships between *Callinectes* larvae in neuston and water column samples; 3) examine the role of certain environmental factors (e.g., temperature, salinity, location) in the distribution and abundance of these larvae; 4) assess the role of *Callinectes* megalopae in larval recruitment and dispersal in view of my findings and results of laboratory studies of temperature-salinity tolerances of larvae; and 5) examine interaction of the developmental migratory sequence, biogeography, and evolutionary history of *Callinectes*.

METHODS

Zooplankton collections were made as part of a 2-yr survey (Table 1) conducted by the Virginia Institute of Marine Science (VIMS) for the Bureau of Land Management (1975-77). This study was designed to provide ecological information prior to drilling for oil on the Middle Atlantic Bight continental shelf. In addition to zooplankton studies the survey included studies of benthic and epibenthic communities and the physical, chemical, and geographical oceanography of the shelf and overlying waters.

During the first year, six stations were occupied seasonally (quarterly) on a transect across the shelf off Atlantic City, N.J. (Figure 1; Table 2: C1, D1, N3, E3, F2, J1). Zooplankton in the water column was sampled at night by paired, double oblique tows with 60 cm diameter, opening-closing bongo nets (McGowan and Brown[5]) (505 μm and 202 μm mesh). Bongo nets were metered (General Oceanics, Inc. flowmeters[6]) and were closed during passage through the surface layer. Neuston was sampled every 3 h over a 24-h period with a neuston net designed at Woods Hole Oceanographic Institution. This sampler consisted of two hydrodynamically-shaped, foam-filled floats connected by an endless fiber glass band (Grant[7]). The mouth of the net was 1.0 m wide, and in calm water the gear sampled approximately the upper 12 cm of the water column. However, the net appeared to sample, on the average, less than the upper 12 cm due to sea conditions and towing characteristics of the ship and sampler. Calculated volumes were based on a 12 cm sample depth and were thus overestimated, resulting in underestimation of

TABLE 1.—Dates for cruises in the Middle Atlantic Bight, 1975-77, over which *Callinectes* larvae were sampled.

Season	First year		Second year	
	Cruise	Date	Cruise	Date
Fall	01W	23-30 Oct. 1975	05W	5-28 Nov. 1976[1]
Winter	02W	5-16 Feb. 1976	06W	20 Feb.-6 Mar. 1977
Spring	03W	8-16 June 1976	07W	18-28 May 1977
Summer	04W	1-9 Sept. 1976	08W	19-29 Aug. 1977

[1]Cruise split into two legs.

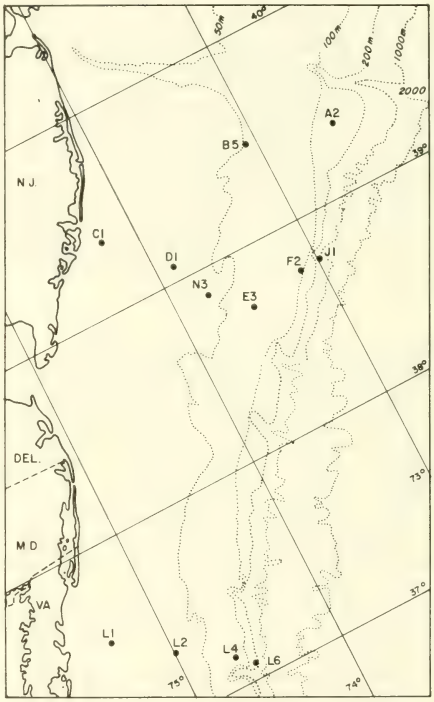


FIGURE 1.—Study area and sampling stations for surface and subsurface zooplankton in the Middle Atlantic Bight, 1975-77. Stations L1, L2, L4, L6, B5, A2 were sampled only during the second year of the study; C1, D1, N3, E3, F2, J1 were sampled both years.

[5]McGowan, J. A., and D. M. Brown. 1966. A new opening-closing paired zooplankton net. Univ. Calif., Scripps Inst. Oceanogr. Ref. 66-23, 56 p.

[6]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[7]Grant, G. C. 1979. Middle Atlantic Bight zooplankton. Spec. Rep. Appl. Mar. Sci. Ocean Eng., Va. Inst. Mar. Sci. 192, 236 p.

TABLE 2.—Station data for zooplankton collections in the Middle Atlantic Bight, 1975-77.

Station	Location		Distance from shore (km)	Bottom depth (m)
	Lat. N	Long. W		
A2	39°21.8′	72°31.8′	149	131
B5	39°28.3′	73°02.1′	93.6	62.6
C1	39°22.2′	74°14.9′	10.2	16.8
D1	39°04.7′	73°53.2′	56.5	37.2
N3	38°51.4′	73°44.8′	83.4	44.7
E3	38°41.2′	73°32.5′	112	59.5
F2	38°44.4′	73°09.2′	132	108
J1	38°44.2′	73°00.7′	141	355
L1	37°31.1′	75°18.3′	31.5	22.3
L2	37°20.1′	74°58.6′	65.8	41.3
L4	37°08.1′	74°36.8′	105	94.6
L6	37°04.4′	74°33.1′	113	322

larval densities. Tows were of 20-min duration except when large abundances of neuston required premature termination of a tow. The net was metered beginning with the June 1976 cruise; before that cruise, sample volumes were estimated on the basis of a standard 20-min tow. Tows were made from an extended boom alongside the ship at speeds of 1.5-2.5 kn.

During the second year two stations to the north and a transect to the south of the original transect were added. On each cruise neuston samples were taken over 24 h at nine stations (Figure 1; Table 2: A2, B5, C1, E3, J1, L1, L2, L4, L6). A single neuston tow was made at stations D1, N3, and F2 as a companion to bongo tows. Bongo tows were made at all 12 stations following the procedure used during the first year. In addition, replicate tows were made at stations A2, B5, and E3 (repeated tows of two bongo nets with paired 202 μm and 505 μm mesh nets). Three such replicate tows were made at night at each designated station.

Samples were preserved in a 4% solution of borax-buffered formaldehyde and seawater (Steedman 1976). In the laboratory, major taxonomic groups were quantitatively sorted from whole or split samples (Burrell et al. 1974). Decapods were sorted to species and identified (when possible) on the basis of published descriptions and taxonomic keys.

Megalopae of several taxa, including *Callinectes*, were reared aboard ship to juveniles. Several megalopae were removed from a sample and tentatively identified or identification characters noted. Megalopae were placed in plastic tackle boxes with 505 μm mesh bottoms and the boxes were floated in an aquarium filled with seawater taken in situ. Megalopae were fed *Artemia salina* nauplii and bits of fresh fish meat. Megalopae with the same characteristics as the megalopae used for rearing were fixed and preserved.

Abundance was expressed as number per 100 m^3; for graphical presentation and certain statistical procedures abundance was compressed by the transformation $\log_{10}(X + 1)$. Most statistical procedures were based on station means, with eight neuston collections per station. The distribution of sample means tends to normality as the sample size increases (Snedecor and Cochran 1967), and the logarithmic transformation tends to make variance independent of the mean (Sokal and Rohlf 1969). Based on the F-max test (Sokal and Rohlf 1969), untransformed abundances within stations were very heteroscedastic, while log-transformed abundances at stations with *Callinectes* larvae in at least six samples did not have unequal variances at $P<0.05$. Coefficients of variation for each station were reduced considerably by the log transformation, and abundances appeared better centered about the median based on "box and whisker" diagrams (Tukey 1977). The assumption of a multivariate normal distribution could not be tested for the data set. Significance levels for mulitvariate data are often difficult to interpret; therefore, significance levels, where indicated for parametric procedures, should be taken as a guide.

A larval stage index (LSI) similar to that of Manzi and Maddox (1976) was calculated for several larval types. The LSI is a point along the continuum of development from hatching (first zoea) to juvenile; the LSI characterizes the stage of an average individual of a given species in a sample. It is calculated as a weighted average, i.e.,

$$\mathrm{LSI} = \frac{\sum_{i=1}^{n} i\,S_i}{n\sum_{i=1}^{n} S_i}$$

where i = number of the developmental stage,
n = number of developmental stages, first zoeae through adult,
S_i = abundance of the ith stage.

The LSI is standardized and constrained in the interval 0.0-1.0 by the assignment of a stage number (1> the megalopa) to the adult stage. Thus, an LSI = 0.67 characterizes animals that have completed, on the average, about two-thirds of the developmental sequence from hatching to first crab. The LSI is, however, a measure of central tendency and does not indicate statistical dis-

persion. Based on Costlow and Bookhout (1959), n was set at 10 for eight zoeal stages, a megalopa, and an adult.

Comparisons between *Callinectes* abundance in neuston and bongo (surface vs. subsurface) collections at each station were made for: 1) maximum abundance for each gear type; 2) mean abundance of the consecutive pair of tows with the largest collective abundance; and 3) mean abundance for each gear type. Significance of differences for these means was determined by the Wilcoxon signed rank test (Wilcoxon 1945), a distribution-free method (Hollander and Wolfe 1973).

Comparisons between neuston and bongo collections are comparisons between abundances in a single "layer" and abundances integrated over the water column. Therefore, abundances in bongo collections represent mean abundances in the water column (excepting the surface) and do not indicate vertical distribution of the animals.

Diel patterns in neuston abundance during each cruise were represented by total numbers per 100 m^3 for each sampling time interval (3 h) summed over the stations in a cruise. To weight frequency as well as abundance during a single cruise, ranks were assigned to abundance during each time interval (lowest to highest) at each station. The rank sum of each time interval was calculated as the sum of the ranks during that time interval over all stations during a single cruise.

For neuston collections the relationship between mean abundance per station and environmental factors (temperature, salinity, station depth, and distance from shore) was examined. Data were analyzed using subprograms (multiple) Regression and Partial Corr (partial correlation) of the Statistical Package for the Social Sciences (SPSS, Nie et al. 1975). Relationships between abundance and factors were examined in terms of bivariate as well as multivariate distributions.

RESULTS

Identification

Callinectes zoeae were identified and staged on the basis of Sandifer's (1972) key and descriptions of laboratory-reared zoeae of *C. sapidus* (Costlow and Bookhout 1959) and *C. similis* (Bookhout and Costlow 1977). Key characters include: 1) relative length of the antennal exopodite (<⅓ protopodite length) and the presence of two unequal terminal setae on the antennal exopodite; 2) the presence of lateral projections on abdominal somites 2 and 3; 3) the presence of relatively long, sharply pointed posterolateral spines on abdominal somites 3-5; and 4) the presence of one dorsal and one lateral spine in each telson furca. Structure and setation of mouthparts and appendages were compared with published descriptions for further confirmation. The above characters effectively separated *Callinectes* zoeae from all other zoeal types in my collections. The planktonic material appeared to include seven or eight distinct zoeal stages after allowance for individual variation in certain structures, setal counts, relative lengths, etc. (e.g., the antennal endopodite "bud" denoting stage 5, which varied from little more than a swelling to a definite projection).

Identification of Portunidae megalopae was based on Kurata's (1975) list of familial and subfamilial (Portuninae) characters, which include the presence of sternal cornua (paired spines projecting posteriorly from the fourth sternal segment beyond the base of the fifth leg) (Figure 2), and the presence of paddlelike dactyls with long, hooked setae on the fifth pereopods.

Callinectes and *Portunus* megalopae were separated on the basis of the characters listed by Bookhout and Costlow (1974), which include the absence in *Callinectes* and the presence in *Portunus* of a ventral spine on the coxa of the second pereopod (Figure 2), and carpal spine(s) on the first pereopod.

My collections included numerous megalopae attributable to *Portunus*; all had a coxal spine on the second pereopod and a carpal spine on the first pereopod. The basischiopodite hook reported for

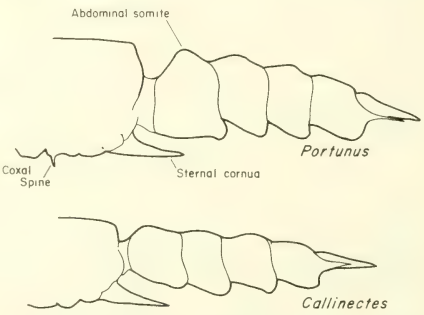


FIGURE 2.—Lateral profile including the abdomen of *Callinectes* and *Portunus* megalopae. Distinguishing characters are indicated. Sizes are not relative.

Portunus (Bookhout and Costlow 1974; Kurata 1975) and *Callinectes* (Costlow and Bookhout 1959; Bookhout and Costlow 1977) was present for all *Callinectes* and most, but not all, *Portunus* specimens.

The profile of abdominal somites was a more subjective, yet reliable, criterion for the separation of *Portunus* and *Callinectes* megalopae. In *Portunus* the dorsal surface of each somite, particularly the first, was noticeably raised, creating a "bumpy" profile; in *Callinectes* the profile was noticeably smoother (Figure 2). (See also Bookhout and Costlow 1974, fig. 11; 1977, fig. 11.) Although identifications were based on numerous characters, this particular criterion was consistent and reliable.

Carapace lengths ($n = 418$, $\bar{X} = 1.56$, SE = 0.004 mm) of *Callinectes* megalopae (measured dorsally from the base of the rostrum to the posterior edge of the carapace) were slightly less than carapace lengths reported for *C. sapidus* ($\bar{X} = 1.65$ mm) but considerably greater than lengths reported for laboratory-reared *C. similis* ($\bar{X} = 1.30$ mm) (Bookhout and Costlow 1977).

I recognized no specific differences among *Callinectes* megalopae or zoeae; therefore, larvae referred to as *Callinectes* may represent more than one species. Abundance and known distribution of adults (Williams 1974) indicated that most, if not all, specimens were *C. sapidus*. Several small adult *C. similis*, however, were taken in neuston collections at station C1 in late October 1975.

The above characteristics used to separate *Callinectes* and *Portunus* megalopae were confirmed by specimens reared to the juvenile stage. *Portunus* juveniles were too small (<10 mm carapace width) for specific identification. One *Callinectes* megalopa developed to a juvenile stage tentatively identified as *C. sapidus*.

Distribution

Callinectes larvae were collected on six of eight cruises and were most abundant in late summer (Figure 3).

Mean abundance in neuston collections ($n = 8$) at a single station reached 3,100/100 m^3 at L2 in August 1977; at this station abundance in a single neuston collection reached a peak of 16,000/100 m^3. Abundance generally decreased offshore of the 50 m isobath during the summer-fall cruises (station J1 in August 1977 was an exception). During the second year, with additional stations, larvae were generally more abundant at stations on the most southern transect than at more northerly stations. Peak abundance often coincided with depressed LSI's inshore, evidence that reproductive activity inshore closely preceded the sampling periods. Except during the summer, larval populations consisted almost exclusively of late zoeae and megalopae, particularly in central and outer shelf waters. Collections of *Callinectes* during the fall of 1975 and winter and spring of 1977 comprised only megalopae.

Mean and maximum abundance (Figure 3; Table 3) was greater in neuston than in bongo collections except at three stations during summer 1977 (Figure 3). During winter 1977, occurrences were too few to be tested at the 0.05 confidence level by the signed rank test. On all other cruises during which *Callinectes* larvae occurred, abundance was significantly greater in surface than subsurface collections (Table 3).

Diel patterns in neuston abundance of *Callinectes* were not consistent over all cruises (Figure 4). A dawn peak in abundance was evident in summer 1976. Dusk peaks appeared in fall 1975 and possibly spring 1977. Total abundance was greatest during darkness (between sunset and

TABLE 3.—Comparison of surface and subsurface (neuston vs. bongo) abundance of *Callinectes* larvae, based on the signed rank test (Wilcoxon 1945). N denotes greater abundance in neuston, significance level indicated by asterisks (* = 0.05, ** = 0.01); P is the probability of a rank sum equal or greater under the null hypothesis of equal surface and subsurface abundance; fraction in parentheses: numerator is the number of occurrences in particular abundance category and denominator is the number of possible occurrences in abundance category.

Comparison	Season and year of collection					
	Fall 1975	Summer 1976	Fall 1976	Winter 1977	Spring 1977	Summer 1977
Maximum neuston vs. maximum bongo	N* $P = 0.016$ (6/6)	N* $P = 0.016$ (6/6)	N** $P = 0.004$ (8/12)	N $P = 0.062$ (4/12)	N* $P = 0.016$ (6/12)	N** $P = 0.008$ (12/12)
Maximum consecutive pair of neuston tows vs. bongos, mean	N* $P = 0.016$ (6/6)	N* $P = 0.016$ (6/6)	N** $P = 0.008$ (7/9)	N $P = 0.125$ (3/9)	N* $P = 0.016$ (6/9)	N** $P = 0.004$ (9/9)
Neuston vs. bongos, mean	N* $P = 0.016$ (6/6)	N* $P = 0.016$ (6/6)	N** $P = 0.008$ (7/9)	N $P = 0.125$ (3/9)	N* $P = 0.016$ (6/9)	N** $P = 00.10$ (9/9)

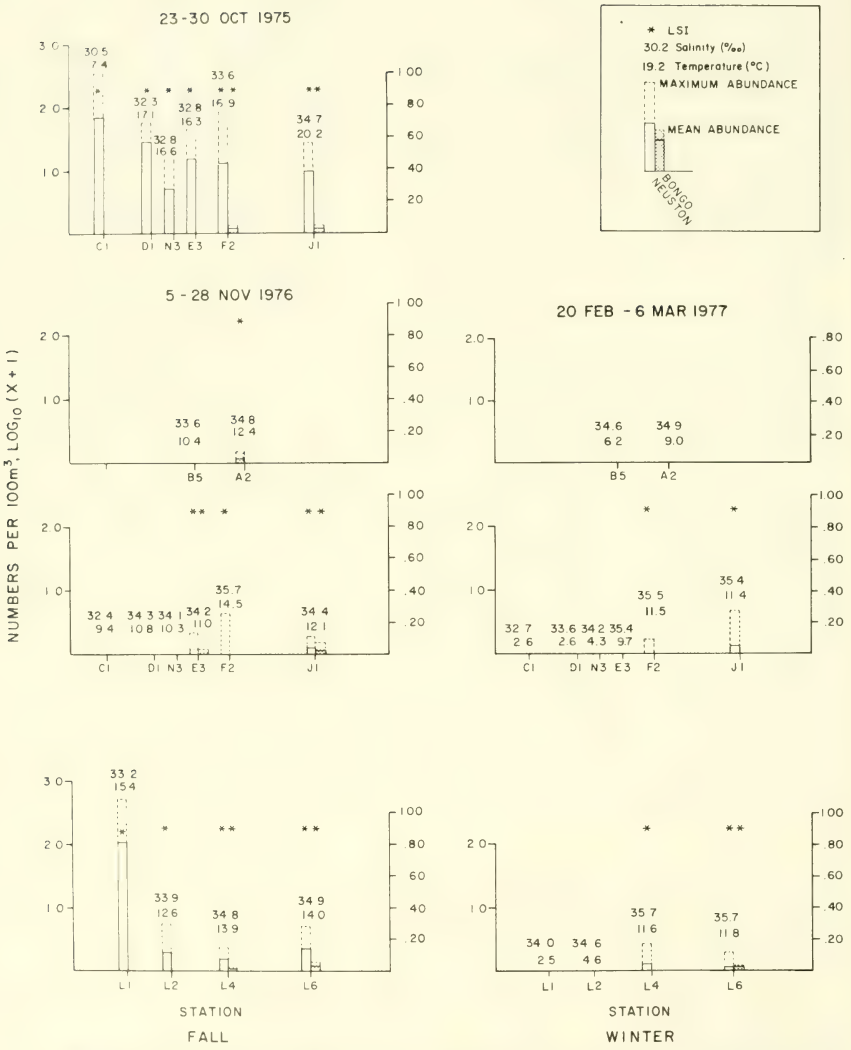
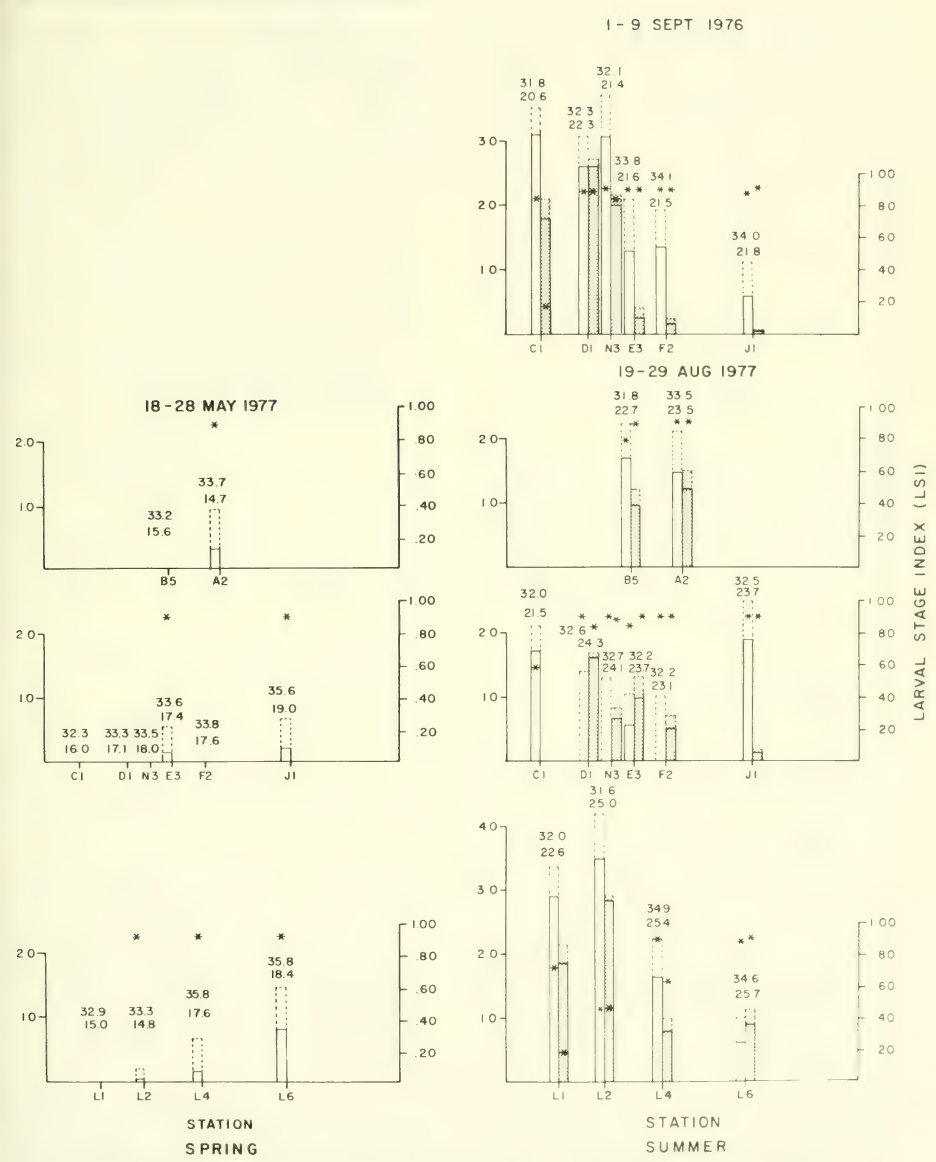


FIGURE 3.—Abundance and larval stage indices (LSI) of *Callinectes* larvae in surface and subsurface collections in



the Middle Atlantic Bight, 1975-77. Stations are ordered by increasing depth on a logarithmic scale within each graph.

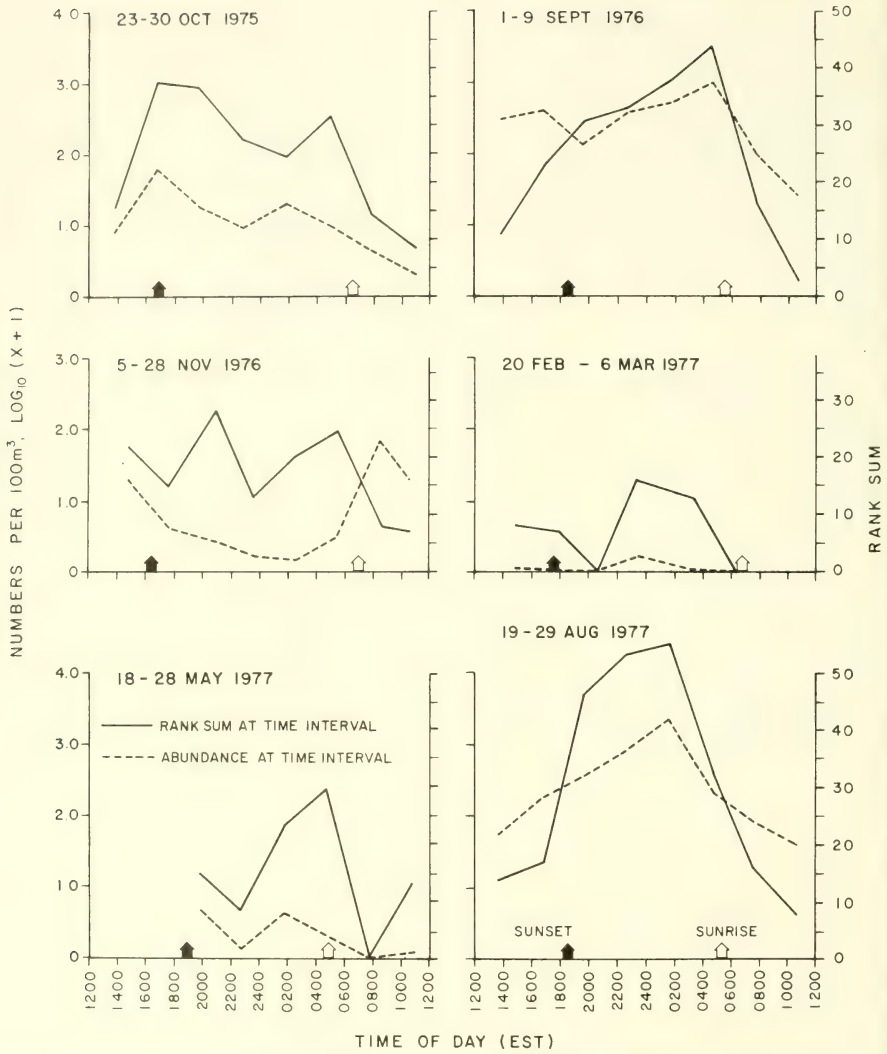


FIGURE 4.—Diel changes in abundance of *Callinectes* larvae in neuston collections in the Middle Atlantic Bight, 1975-77. Abundance (dashed line) for each time interval was averaged over the stations of a cruise. The rank sum for each cruise (solid line) was calculated by summing over all stations the ranks (lowest to highest) of the abundances at each time interval. (The rank sum weights the frequency of occurrence at each time interval.)

sunrise) on all cruises except fall 1976, when abundance was greatest during daylight hours. The rank sum, which weights both abundance and frequency of occurrence, indicated patterns of

diel change similar to diel patterns of total abundance—except during fall 1976. As distance from shore increased and abundance decreased, however, *Callinectes* larvae (late zoeae and megalopae) were generally collected at the surface only at night. Ten of 15, and 10 of 12 occurrences (megalopae) during winter and spring 1977 were at night.

Larvae were taken at salinities ranging from 30.5 to 35.8‰ and temperatures from 11.0° to 25.7° C (surface temperature and salinity); peak abundance occurred in the ranges 31.6-34.9‰ and 20.6°-25.7° C. Mean temperature, salinity, and distance from shore, weighted for abundance, for all neuston collections of *Callinectes* larvae were 22.9° C, 31.9‰, and 55.9 km. Plots of temperature and salinity vs. abundance indicated no clear relationships among these variables.

For the independent variables—temperature, salinity, distance from shore, and depth—simple (bivariate) correlation analysis indicated strongest correlation between mean neuston abundance per station and salinity and weakest correlation of abundance with bottom depth (Table 4).

TABLE 4.—Simple correlation matrix for surface abundance of *Callinectes* larvae and selected environmental variables.

Variable	Abundance ($\log_{10}[X+1]$)	Temperature (°C)	Salinity (‰)	Distance from shore (km)
Temperature	0.6260***			
Salinity	-0.7086***	-0.5133**		
Distance from shore	-0.5812***	-0.1695	0.6259***	
Bottom depth	-0.4024**	-0.1218	0.5621**	0.6261***

**$P<0.01$, ***$P<0.001$.

When considered together, the variables form a multivariate population. Partial correlation analysis (Table 5) indicated a very weak relationship between bottom depth and larval abundance for all second and third, and most first order correlations. Depth was, therefore, deleted from further analysis. Second order correlations among temperature, salinity, and distance from shore revealed strongest correlation of abundance with temperature, followed by distance from shore and salinity.

Based on partial correlation analysis, independent variables were entered into a multiple regression equation in the order temperature, distance from shore, salinity, and depth. These variables explained 66.0% of the variation in abundance (Table 6), the maximum possible for any linear combination of these variables. Depth contributed negligibly to explained variance, and salinity very little (Table 6). The regression equation containing only the variables temperature and distance from shore, explaining 62.4% of the variation in abundance, is

$$A = 0.1393 + 0.1124T - 0.0115D$$

where A = abundance ($\log_{10}[X + 1]$),
T = temperature in degrees Celsius,
D = distance from shore in kilometers.

The regression of abundance on temperature and distance from shore was highly significant (Table 7).

TABLE 5.—Partial correlation coefficients for surface abundance $\log_{10}[X+1]$ of *Callinectes* larvae with selected environmental variables.

Temperature (°C)	Salinity (‰)	Distance from shore (km)	Bottom depth (m)
First order correlations:			
c[1]	-0.5787	-0.6182	-0.4214
0.4331	c	-0.2502	-0.0069
0.6577	-0.5434	c	-0.0606
0.6350	-0.6372	-0.4613	c
Second order correlations:			
c	c	-0.3969	-0.1240
c	-0.3051	c	-0.0627
c	-0.4514	-0.5017	c
0.5194	c	c	0.1135
0.4472	c	-0.2732	c
0.6578	-0.5493	c	c
Third order correlations:			
c	c	c	0.0378
c	c	-0.3815	c
c	-0.3013	c	c
0.5112	c	c	c

[1]c indicates variable which is controlled (effects removed).

The regression of abundance on temperature and distance from shore was highly significant (Table 7).

The temperature-distance from shore-abundance relationship for all cruises is summarized in Figure 5. Summer collections formed a unique group, distributed across the shelf. Abundance appeared relatively uniform at least to a distance of 100 km from shore, with a slight increase at the outermost stations. Temperature did not appear to be a limiting factor for these summer collections. Relationships are less clear for other seasons. Fall collections generally decreased in abundance with decreasing temperature and increasing distance from shore. Winter and spring collections formed groups which were limited to the outer shelf.

Cooccurring Decapods

Collections made during periods of peak abundance of *Callinectes* (in the summer) included

TABLE 6.—Variation explained by multiple regression of surface abundance ($\log_{10}[X + 1]$) of *Callinectes* larvae on temperature, distance from shore, salinity, and depth as estimated by the coefficient of determination (r^2). Data were entered in the order indicated in the Statistical Package for the Social Sciences (Nie et al. 1975) stepwise multiple regression procedure.

Temperature, distance from shore, salinity, depth			Salinity, temperature, distance from shore, depth		
Variable	r^2	Δr^2	Variable	r^2	Δr^2
Temperature (°C)	0.3919	0.3919	Salinity	0.5021	0.5021
Distance from shore (km)	0.6243	0.2324	Temperature	0.5955	0.0934
Salinity (‰)	0.6592	0.0350	Distance from shore	0.6592	0.0637
Bottom depth (m)	0.6597	0.0005	Bottom depth	0.6597	0.00049

TABLE 7.—ANOVA table for regression of surface abundance ($\log_{10}[X+1]$) of *Callinectes* larvae on temperature and distance from shore.

Source of variation	Degrees of freedom	Sum of squares	Mean square	F
Total	41	37.23161	0.908088	
Regression	2	23.24224	11.62112	32.39773***
Residual	39	13.98937		

***$P < 0.001$.

peak abundances of inshore and estuarine genera such as *Uca* (zoeae and megalopae), *Emerita* (zoeae), *Palaemonetes* (zoeae), *Upogebia* (zoeae), *Libinia* (zoeae and megalopae), and *Ovalipes* (zoeae and megalopae). Few of the above were found beyond the inner shelf (Figure 1: C1, D1, L1). At offshore stations *Callinectes* larvae frequently occurred with larvae of shelf forms such as *Cancer*, which dominated neuston collections made in the spring. Megalopae and a few zoeae of *Portunus* usually occurred with *Callinectes*. Megalopae of *Ocypode quadrata* were ubiquitous across the shelf during summer 1977. Megalopae of *Dromidia antillensis* and other forms of southern origin often occurred at central and outer shelf stations.

DISCUSSION

Temperature-salinity tolerances of *Callinectes* larvae are available from several laboratory and field studies. Optimum temperature-salinity ranges, experimentally determined, for survival during zoeal development of laboratory-reared *C. sapidus* were 21-28‰, 19°-29° C (Sandoz and Rogers 1944) and 20-32‰ at 25° C (Costlow and Bookhout 1959). Sandifer (1972) collected *C. sapidus* zoeae in Chesapeake Bay in the range 15.7-32.3‰ (most at 20-30‰) and 14°-27.9° C (75% at 25°-26° C). Nichols and Keney (1963) found larvae (zoeae and megalopae) to be most abundant offshore (Florida-North Carolina) at 27.3°-29.1° C and least abundant at 14.3°-16.4° C.

Costlow (1967) reported survival of megalopae to first crab in temperature-salinity combinations of 15°-30° C, 5-40‰. Survival was similar at 20°, 25°, and 30° C, 10-40‰ (75% survival) and occurred at salinities as low as 5‰ at 25°-30° C. Survival in the lower salinity ranges (5-10‰) increased with increasing temperature to 95% at 30° C, 10‰. Survival in the upper salinity ranges (30-35‰) decreased from 95-100% at 25° C to 42-50% at 15° C. At 15° C larvae did not survive below 20‰, and at 15° C survival was highest at 35‰ (50%).

Costlow and Bookhout (1959) found zoeal development to require 31-49 days, with no significant difference in larval duration at salinities from 20.1 to 31.1‰ (at 25° C). Duration of the megalopal stage ranged from 5-11 days at 30° C (5-40‰) to 30-67 days at 15° C (20-40‰) (Costlow 1967). Costlow (1967) reported significant interaction between temperature and salinity only at 15° C. Larval duration at 35‰, 15° C was 37-56 days. Costlow (1967) did not rear larvae at temperatures <15° C and did not include a regression equation for extrapolation to lower temperatures.

Based on experimentally determined tolerances noted above, summer temperatures in the estuaries and inshore waters along most of the middle Atlantic and southeastern U.S. coast are sufficiently warm for completion of larval development. Metamorphosis of megalopae may occur during the warmer months at salinities found from offshore to upper estuaries. Greatest survival, however, is at higher salinities (30-40‰), and at 15° C occurs only in the range of oceanic salinities. Furthermore, at these oceanic salinities the duration of the megalopal stage increases as temperature decreases. Thus, megalopal life may be extended in the cooler, offshore water of the Middle Atlantic Bight, a conclusion supported by the presence of *Callinectes* megalopae at outer shelf stations (11°-12° C, 35-36‰).

Results of multivariate analysis of data were predictable (Figure 5; Tables 5-7). The importance of temperature (positive correlation) reflected the seasonal nature of spawning and development (in

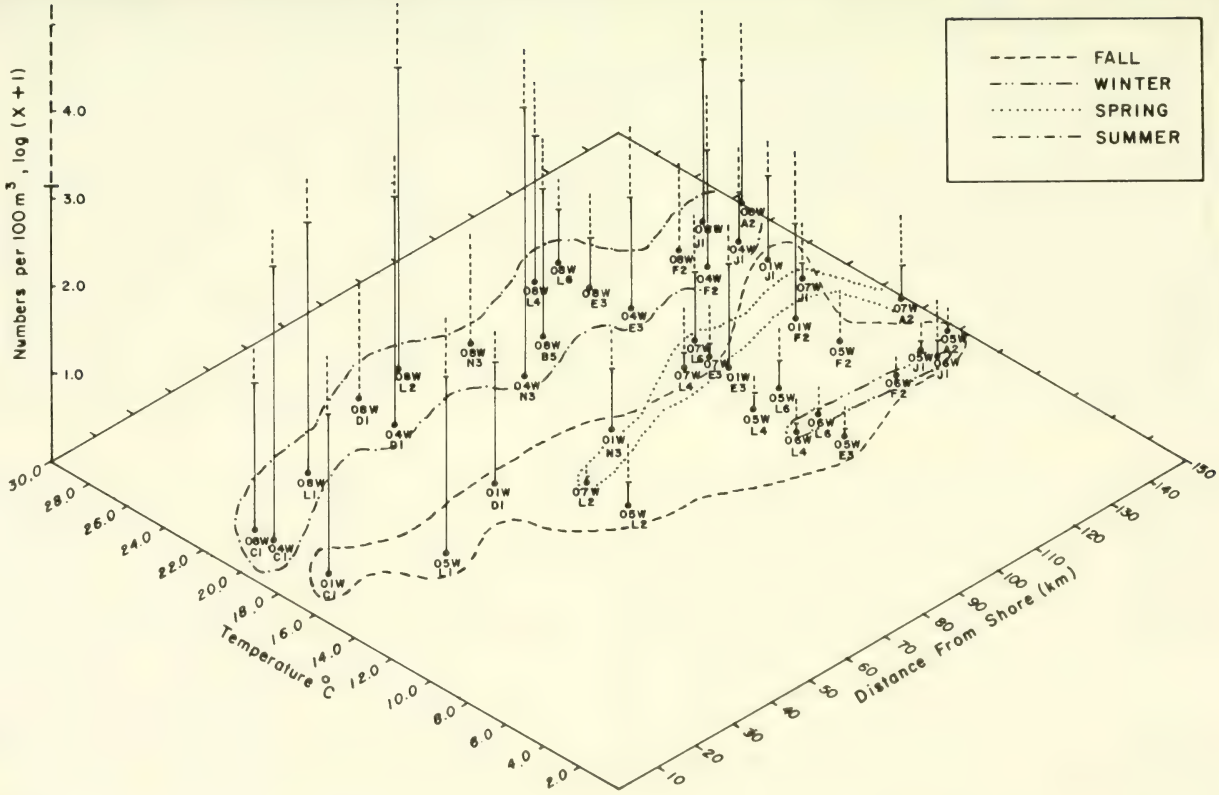


FIGURE 5.—Temperature-distance from shore-abundance diagram for *Callinectes* larvae in neuston collections in the Middle Atlantic Bight, 1975-77. Abundance is indicated on the vertical scale by a solid line for mean abundance and dashed line for maximum abundance. Stations (under cruise numbers) are grouped by season within broken lines.

summer). The secondary importance of distance from shore (negative correlation) was reflected in decreasing abundances with increasing distance from shore. Because all collections were made well within the range of optimum salinities for development, salinity could have been expected to contribute little to explained variation in abundance.

Results of multivariate analysis of data emphasize that a bivariate approach to multivariate data can be misleading. Salinity had the highest simple correlation (−0.7086; Table 4) with abundance. Consequently, in the usual SPSS stepwise multiple regression procedure (Nie et al. 1975) salinity would be entered as the first variable in the analysis. The proportion of variation (r^2, Δr^2) in abundance explained by temperature, distance from shore, salinity, and depth was quite in contrast to proportions of explained variance when salinity, rather than temperature, was entered first in the multiple regression equation (Table 6).

The relative importance of temperature, distance from shore, and salinity was best illustrated by partial correlation coefficients (Table 5). This procedure examines correlation between two variables when the effect of other variables is controlled. I recommend partial correlation as a preliminary step to multiple regression procedures and as more appropriate than bivariate procedures.

This paper reports for the first time the existence of a large population of *Callinectes* larvae in offshore shelf waters of the Middle Atlantic Bight. The presence of an offshore population, necessary to the accepted model of larval distribution, has had relatively little documentation. Nichols and Keney (1963) found advanced stages of *Callinectes* as far as 64-97 km offshore, with greatest abundance at stations 32 km offshore. Dudley and Judy (1971) reported zoeae, chiefly stage III and earlier, and a few megalopae at stations 10-13 km offshore. Tagatz (1968) reported a few megalopae as far upstream as 40 km in the St. Johns River, Fla., and Williams (1971) collected megalopae ". . . almost the entire length of the [North Carolina] estuary."

Abundance reported here (Figure 3) is somewhat less than that previously reported. Sandifer (1972) and Tagatz (1968) reported maximum larval abundance of 42,000 and 46,100/100 m^3, respectively, and Dudley and Judy (1971) reported maximum abundance of 105,000/100 m^3. These data, however, included few megalopae. Williams (1971) found considerably greater numbers of megalopae than did previous workers but reported abundance as numbers per sample (10's-1,000's).

My results confirm the reported affinity of *Callinectes* larvae, particularly megalopae, for surface layers. Previously Sandifer (1972) reported that 89.4% of the *Callinectes* larvae that he collected were from surface samples but reported only three occurrences of megalopae, all in bottom samples. Dudley and Judy (1971) found, overall, more *Callinectes* larvae in surface (1.0 m) than in subsurface (8.0 m) collections except at offshore (10-13 km) stations. They collected advanced zoeae (their last three stages) only at offshore stations. Tagatz (1968) collected more zoeae at the surface than at the bottom, and Williams (1971) reported *Callinectes* megalopae to be active at night in surface waters. The results of these studies, however, reflect differences in gear types, mesh sizes, and sampling design; gear specifically designed to sample surface layers was in no case employed.

Reasons for the affinity of *Callinectes* and other megalopae for the neuston are not readily apparent. Diel increases in abundance in night collections of neuston may indicate a negative phototropic response or possibly net avoidance in the daytime. Numerous holoplankters (copepods, etc.) exhibit the same diel pattern, and the upward movement of megalopae may be related to feeding strategies. It is not surprising that of the megalopae collected in this study, the Portunidae (swimming crabs) showed the strongest affinity for the neuston. Megalopae of other crabs, however, such as *Cancer*, *Ocypode*, and *Dromidia* also showed strong surface affinities.

Spatial distribution of plankton in shelf waters is largely determined by circulation patterns. With cross-shelf flow in the Middle Atlantic Bight offshore at the surface and onshore at depth (Bumpus 1973), coastal organisms in the surface layers would be transported offshore, with the possibility of return at depth. A coastal boundary layer, a band of trapped nearshore flow some 10 km wide, has been reported off New Jersey (Csanady 1976). Coastal boundary layers are associated with the upwelling of cold water as a consequence of the offshore movement of surface waters and subsequent thermocline tilt (Csanady 1976). Most coastal and estuarine larvae in my collections (species of *Uca*, *Palaemonetes*, *Libinia*, etc.) were infrequent seaward of station C1 and are evidently retained within this zone. Late stage

Callinectes larvae were most abundant outside the coastal boundary layer in my collections as well as in those of Nichols and Keney (1963). *Callinectes* juveniles or adults were not collected during this study in extensive benthic sampling (otter and small biological trawls, dredge and grab samplers), and small adults were collected only once in plankton samples (*C. similis*, $n = 5$, station C1, neuston, October 1975). Thus, this study presents no evidence for recruitment to inshore and estuarine populations, either by juveniles or megalopae; the evidence, however, does not preclude recruitment from the offshore larval population.

General longshore drift in the Middle Atlantic Bight is southwestward (Iselin 1955; Harrison et al. 1967; Bumpus 1973; and others) and may occur as sporadic events rather than in a continuous sweep (Ruzecki et al. 1976). Reversals of the longshore flow, usually confined to a narrow belt close inshore, may occur from April to September (Bumpus 1969, 1973). A general constraint, however, seems to be placed on larval origins, viz. adult populations are more likely to be replenished by recruitment from larval populations spawned to the north. Given a mean longshore drift of 5 cm/s (Bumpus 1973) and a megalopal duration of 5-67 days (Costlow 1967), a megalopa has a range of 22-290 km; at inshore temperature-salinity ranges (20°-25° C, 30-35‰) a megalopa might be transported 26-56 km.

Callinectes megalopae collected on the outer shelf in the winter and spring, as well as some megalopae found there in the summer and fall, probably have southern origins. Water masses of Gulf Stream origin, as meanders and warm-core eddies, have frequently been observed in the slope-outer shelf regions (Saunders 1971; see Wright 1976 for a review). Although large-scale, long-range transport is not evident, the presence of *Callinectes* and *Portunus* megalopae at station J1 in the winter indicates either transport from the south or, less plausibly, delayed metamorphosis of megalopae from Middle Atlantic Bight populations as a result of low winter temperatures. Based on Costlow's (1967) response surfaces, a megalopa in Gulf Stream waters would have a duration of 7-26 days and a range, at 2 kn, of 600-2,300 km. Thus, some megalopae in the Middle Atlantic Bight may originate from late spawning populations to the south. Metamorphosis would be further delayed by depressed temperatures of shelf and slope waters. The presence of definite southern larval forms (e.g., *Dromidia*) in outer shelf collections supports the hypothesis that at least some of the *Callinectes* and other megalopae were produced by southern crab populations.

The developmental model of *Callinectes*, i.e., larval development in shelf waters and subsequent recruitment to inshore and estuarine adult populations, reflects the evolutionary history of the group. Portunids are "reproductively conservative," migrating to waters of oceanic, or near oceanic, salinities to release larvae (Norse 1977). Williams (1974) described *Callinectes* as "a portunid group evolving at the geographic limits of the family, specializing in occupation of estuaries, ..." In this light, the migratory sequence of larval stages is a response to the problems of an essentially marine group invading the estuaries. Spawning areas (marine) may represent a primitive condition, and the spatial sequence of stages returns larvae to habitats in which the adults are successful. It is, as Williams (1974) described it, a "homeostatic developmental feature in the life histories of the species" that has not been carried to an evolutionary conclusion, that is, retention within the estuary for the entire life history.

It can be argued that such a model of development may in part account for the success and widespread distribution of *Callinectes*. If, as Norse (1977) and others have indicated, recruitment occurs through metamorphosis of megalopae rather than immigration of adults, then such a sequence would allow dispersal into numerous estuaries yet assure genetic continuity over broad areas. Such a role has been suggested by Cole and Morgan (1978). Furthermore, it would seem more likely that this is a primitive mechanism retained, rather than developed, through selection pressures.

The essential features of *Callinectes* development appear to be spawning and hatching in or near the primitive habitat (along the shore) during most of the warmer months, maintenance of a large larval population in the shelf waters (chiefly in the surface layers), recruitment from the larval pool, and exploitation of the estuarine habitat as adults.

There is, however, a paradox in the biogeography of *Callinectes* and the spatial sequence of developmental stages. Given the southern affinities of the genus and general southerly longshore movement of waters along most of the

U.S. Atlantic shelf, the distribution of *Callinectes* is counter to the direction of immediate larval transport. Recruitment to adult populations at the northern limits of *Callinectes* is problematical. Not all larvae can originate from parental stocks to the north. This may indicate that recruitment takes place from megalopal populations closer inshore than those reported in this study and by Nichols and Keney (1963), with the coastal boundary layer possibly retaining larvae. The megalopae collected farther offshore may represent larval wastage to parental populations (but not necessarily to the species).

ACKNOWLEDGMENTS

I wish to thank John Olney, Steve Berkowitz, Cathy Womack, Mike Vecchione, and Roberta Wallace for assistance in making collections. Shelia Berry, Pat Crewe, Roberta Wallace, and JoEllen Sanderson capably sorted the samples. I thank Jacques van Montfrans, W. A. Van Engel, George Grant, Morris Roberts, and two anonymous reviewers for their critical review of the manuscript and helpful comments and suggestions. I also thank Shirley Sterling and Ruth Edwards for typing the various drafts. Mary Jo Shackelford and June Hoagman prepared the final figures. Final copy of this manuscript was prepared by the VIMS Report Center. This research was supported in part by contract no. 08550-CT5-42 and AA550-CT6-62 from the Bureau of Land Management, U.S. Department of Interior.

LITERATURE CITED

BANSE, K.
1975. Pleuston and neuston: on the categories of organisms in the uppermost pelagial. Int. Rev. gesamten Hydrobiol. 60:439-447.

BERKOWITZ, S. P.
1976. A comparison of the neuston and near-surface zooplankton in the northwest Gulf of Mexico. M.S. Thesis, Texas A&M Univ., College Station, 148 p.

BOOKHOUT, C. G., AND J. D. COSTLOW, JR.
1974. Larval development of *Portunus spinicarpus* reared in the laboratory. Bull. Mar. Sci. 24:20-51.
1977. Larval development of *Callinectes similis* reared in the laboratory. Bull. Mar. Sci. 27:704-728.

BUMPUS, D. F.
1969. Reversals in the surface drift in the Middle Atlantic Bight area. Deep-sea Res. Oceanogr. Abstr. Suppl. 16:17-23.
1973. A description of the circulation on the continental shelf of the east coast of the United States. Prog. Oceanogr. 6:111-157.

BURRELL, V. G., JR., W. A. VAN ENGEL, AND S. G. HUMMELL.
1974. A new device for subsampling plankton samples. J. Cons. 35:364-366.

COLE, M. A., AND R. P. MORGAN, II.
1978. Genetic variation in two populations of blue crab, *Callinectes sapidus*. Estuaries 1:202-205.

COSTLOW, J. D., JR.
1967. The effect of salinity and temperature on survival and metamorphosis of megalops of the blue crab *Callinectes sapidus*. Helgol. wiss. Meeresunters. 15:84-97.

COSTLOW, J. D., JR., AND C. G. BOOKHOUT.
1959. The larval development of *Callinectes sapidus* Rathbun reared in the laboratory. Biol. Bull. (Woods Hole) 116:373-396.

CSANADY, G. T.
1976. Wind-driven and thermohaline circulation over the continental shelves. *In* B. Manowitz (editor), Effects of energy-related activities on the Atlantic Continental Shelf, p. 31-47. Conference at Brookhaven National Laboratory, November 10-12, 1975. Available Natl. Tech. Inf. Serv., Springfield, Va., as BNL 50484.

DUDLEY, D. L., AND M. H. JUDY.
1971. Occurrence of larval, juvenile, and mature crabs in the vicinity of Beaufort Inlet, North Carolina. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-637, 10 p.

GOY, J. W.
1976. Seasonal distribution and retention of some decapod crustacean larvae within the Chesapeake Bay, Virginia. M.S. Thesis, Old Dominion Univ., Norfolk, Va., 334 p.

HARRISON, W., J. J. NORCROSS, N. A. PORE, AND E. M. STANLEY.
1967. Circulation of shelf waters off the Chesapeake Bight. Surface and bottom drift of continental shelf waters between Cape Henlopen, Delaware, and Cape Hatteras, North Carolina June 1963-December 1964. U.S. Dep. Commer., Environ. Sci. Serv. Adm. Prof. Pap. 3, 82 p.

HOLLANDER, M., AND D. A. WOLFE.
1973. Nonparametric statistical methods. Wiley, N.Y., 503 p.

ISELIN, C. O'D.
1955. Coastal currents and the fisheries. Deep-Sea Res. Suppl. 3:474-478.

KURATA, H.
1975. Larvae of Decapoda Brachyura of Arasaki, Sagami Bay - V. The swimming crabs of subfamily Portuninae. Bull. Nansei Reg. Fish. Res. Lab. 8:39-65.

MANZI, J. J., AND M. B. MADDOX.
1976. Algal supplement enhancement of static and recirculating system culture of *Macrobrachium rosenbergii* larvae. Helgol. wiss. Meeresunters. 28:447-455.

MORRIS, B. F.
1975. The neuston of the northwest Atlantic. Ph.D. Thesis, Dalhousie Univ., Halifax, 285 p.

NICHOLS, P. R., AND P. M. KENEY.
1963. Crab larvae (*Callinectes*), in plankton collections from cruises of M/V *Theodore N. Gill*, South Atlantic coast of the United States, 1953-54. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 448, 14 p.

NIE, N. H., C. H. HULL, J. G. JENKINS, K. STEINBRENNER, AND D. H. BENT.
1975. SPSS. Statistical package for the social sciences. 2d ed. McGraw-Hill, N.Y., 675 p.

NORSE, E. A.
1977. Aspects of the zoogeographic distribution of *Cal-*

linectes (Brachyura: Portunidae). Bull. Mar. Sci. 27: 440-447.

RUZECKI, E. P., C. WELCH, J. USRY, AND J. WALLACE.
1976. The use of the EOLE satellite system to observe continental shelf circulation. 8th Annu. Offshore Technol. Conf. Proc. 2:697-[708]. Pap. No. OTC 2592.

SANDIFER, P. A.
1972. Morphology and ecology of Chesapeake Bay decapod crustacean larvae. Ph.D. Thesis, Univ. Virginia, Charlottesville, 532 p.

SANDOZ, M., AND R. ROGERS.
1944. The effect of environmental factors on hatching, moulting, and survival of zoea larvae of the blue crab *Callinectes sapidus* Rathbun. Ecology 25:216-228.

SAUNDERS, P. M.
1971. Anticyclonic eddies formed from shoreward meanders of the Gulf Stream. Deep-Sea Res. Oceanogr. Abstr. 18:1207-1219.

SNEDECOR, G. W., AND W. G. COCHRAN.
1967. Statistical methods. 6th ed. The Iowa State Univ. Press, Ames, 593 p.

SOKAL, R. R., AND F. J. ROHLF.
1969. Biometry. The principles and practice of statistics in biological research. W. H. Freeman, San Franc., 776 p.

STEEDMAN, H. F.
1976. General and applied data on formaldehyde fixation and preservation of marine zooplankton. *In* H. F. Steedman (editor), Zooplankton fixation and preservation, p. 103-154. Monogr. Oceanogr. Methodol. 4.

TAGATZ, M. E.
1968. Biology of the blue crab, *Callinectes sapidus* Rathbun, in the St. Johns River, Florida. U.S. Fish Wildl. Serv., Fish. Bull. 67:17-33.

TUKEY, J. W.
1977. Exploratory data analysis. Addison-Wesley, Reading, Mass., 688 p.

WILCOXON, F.
1945. Individual comparisons by ranking methods. Biometrics 1:80-83

WILLIAMS, A. B.
1965. Marine decapod crustaceans of the Carolinas. U.S. Fish Wildl. Serv., Fish. Bull. 65:1-298.
1971. A ten-year study of meroplankton in North Carolina estuaries: annual occurrence of some brachyuran developmental stages. Chesapeake Sci. 12:53-61.
1974. The swimming crabs of the genus *Callinectes* (Decapoda: Portunidae). Fish. Bull., U.S. 72:685-798.

WRIGHT, W. R.
1976. The limits of shelf water south of Cape Cod, 1941-1972. J. Mar. Res. 34:1-14.

ZAITSEV, Y. P.
1970. Marine neustonology (Morskaya neistonologiya). Isr. Programs Sci. Transl. A. Mercado (translator), K.A. Vinogradov (editor), 207 p.

AN ANALYSIS OF THE UNITED STATES DEMAND FOR FISH MEAL

D. D. HUPPERT[1]

ABSTRACT

As fishery management plans are developed under the Fishery Conservation and Management Act of 1976, economic evaluation of management procedures will be necessary. To adequately address the economics of optimum yield, for instance, research will be required in the traditional economic subjects of demand, production and costs, industrial organization, and international trade. This paper addresses the domestic demand for the primary industrial fishery product—fish meal. In developing the demand model the important points are: 1) choice of empirical variables for inclusion in the model, 2) determination of appropriate functional form of the demand equation, 3) treatment of the "simultaneity bias" problem, and 4) choice between a static (or equilibrium) model and a dynamic model. The paper presents maximum likelihood estimates of both the static and dynamic models. With either model the price elasticity of demand is high when fish meal price is low, and is low when price is high.

Analysis of prices and market demand relationships for fish is of increased importance since the enactment of the U.S. Fishery Conservation and Management Act of 1976 (FCMA[2]). The new law not only establishes a zone of Federal control over fisheries from 3 to 200 mi offshore, but it also establishes national standards for fishery management plans which include economic and social aspects. A key concept is that of "optimum yield"—that rate of annual catch "which will provide the greatest overall benefit to the Nation" (FCMA, Sec. 3(18)). Economic benefits to the nation accrue primarily through the consumption of fishery products which are sold in more-or-less free and competitive markets. Market prices can be expected to vary in response to changes in the annual yields permitted under fishery management plans. These price impacts, along with associated changes in real income, cannot be neglected in the development of appropriate management methods. The demand analysis presented in this paper will assist in the determination of optimum yield for fisheries which contribute to the U.S. fish meal supply.

Fish meal is a primary product of the Atlantic and Gulf of Mexico menhaden fisheries and the California anchovy fishery. It also appears as a byproduct of groundfish and tuna processing. It is used as a high protein supplement most commonly mixed with corn, soybean, or cottonseed meal; meat byproduct meal; and vitamins and minerals for feeding to broilers, layers, and turkeys. According to J. Vondruska,[3] fish meal is also used in feeds for mink and other fur-bearing animals, farmed fish, laboratory animals, livestock, and household pets. About 80% of fish meal consumed in the United States goes into poultry feed. A high level of metabolizable energy and such nutritional elements as riboflavin, pantothenic acid, niacin, choline, and several amino acids are contributed to animal feed by the addition of fish meal (Karrick 1963). Most of these constituents are available in high protein vegetable meals, but fish has a particularly high concentration of the amino acids lysine and methionine.

Because the lysine and methionine are necessary for fast growth in chicks, feed mixers generally seek to include between 2 and 8% fish meal in broiler rations. With >8% fish meal, the poultry tends to pick up a "fishy" flavor. With <2% fish meal, further substitution of vegetable protein meals for fish meal will result in slower growth because the fixed quantity of feed eaten per day per chick cannot contain the ideal mix of amino acids. When fish meal is extremely high priced or

[1]Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, CA 92038.

[2]Public Law 94-265, 94th Congress, 2d Session 13 April 1976, 16 USC 1801 et seq. (Suppl. 1977). Hereafter, FCMA.

[3]J. Vondruska. 1979. Postwar production, consumption, and prices of fish meal. Unpubl. manuscr., 66 p. National Marine Fisheries Service, 3300 Whitehaven St., N.W., Washington, DC 20235.

Manuscript accepted November 1979.
FISHERY BULLETIN: VOL. 78, NO. 2, 1980.

unavailable, the lysine and methionine content of the feed can be augmented with synthetic proteins. Kolhonen (1974) described the development of synthetic methionine and lysine for use in feed formulas.

Linear programming has been widely adopted by formula feed manufacturers in the United States and western Europe (Kolhonen 1974). Least-cost combinations of feed constituents needed for adequate nutrition are quickly and accurately computed for any vector of constituent prices. Thus, the demand for feed ingredients is expected to exhibit great sensitivity to relative prices. In a recent examination of demand for agricultural feed ingredients, Meilke (1974) reported that price elasticities are generally >2 in absolute value. It is expected that the demand for fish meal will be elastic also, at least when available quantities allow the feed formula manufacturers to include between 2 and 8% fish meal in poultry rations. When the supply of fish meal is low enough to jeopardize the maintenance of at least 2% fish meal, the demand may become inelastic. Thus, one hypothesis to be tested is that the own price elasticity of demand for fish meal falls with increasing price and decreasing quantity.

Markets for fish meal in the United States are, for obvious reasons, concentrated in the poultry-producing regions—California, Arkansas, and states in the Deep South. Domestic production of fish meal occurs mainly in California, the Gulf Coast States, and the South Atlantic States. In some years, however, much of the domestic supply is imported from major foreign producers such as Peru. Foreign meal is a perfect substitute for the domestic product, but the supply of foreign meal has undergone tremendous fluctuations due to variations in fish stocks (especially the Peruvian anchoveta, *Engraulis ringens*). Domestic supplies have also been strongly influenced by uncontrolled variations in domestic stocks (especially menhaden *Brevoortia tyannus* and *B. patronus*) and by administrative decisions of fishery management agencies (California's anchovy, *Engraulis mordax*, fishery, e.g., see Pacific Fishery Management Council 1978: 31660-31664). On the supply side of the domestic market, therefore, the major fluctuations are not price induced, but are due to exogeneous factors. On the demand side the poultry industry experienced a steady expansion starting in the early 1950's and continuing until about 1970.

DEVELOPMENT OF DEMAND MODEL

Demand and price analysis has been a cornerstone of applied economic research since the 1930's (Working 1927; Schultz 1938; Wold and Juréen 1953). Agricultural economists have been particularly active in developing demand models for commodities. Research on demand for fish is of more recent vintage but differs in few important respects from that for agricultural commodities. For an excellent review of the historical development of demand analysis, see Waugh and Norton (1969). Among the methodological issues addressed in applied demand studies are: 1) specification of the demand model, 2) development of appropriate functional forms, 3) treatment of simultaneity bias in market demand and supply function estimates, and 4) incorporation of dynamic response mechanisms in the demand model. These issues are discussed seriatim.

Specification

The specification of a demand model consists of the choice of dependent and independent variables. Annual quantity demanded, as measured by quantity purchased, should be the dependent variable. Purchased quantities are difficult to obtain, however, while production, import, and export statistics are well documented. Also, meals derived from different sources differ in protein content and sell at different prices. Both the quantities and the prices must be aggregated such that they represent a reasonably homogeneous commodity. Fish meal quantities (Table 1, columns 1-6) are converted to a protein equivalent basis by multiplying the quantity of each type of meal by the prevailing percentage of protein content. The total available domestic quantity, computed by summation of protein equivalent fish meals and subtraction of exports, is listed in Table 1, column 7. Similarly, since the prices of the various fish meal types (Table 2, columns 1-4) are based on protein content, each price is converted to a protein basis. The aggregate price of fish meal introduced as an independent variable in the demand model is the average price per unit protein for all meal supplied to the U.S. market (Table 2, column 5). Some specification error may enter the model because domestic supply rather than quantity purchased is used for the dependent variable, but this problem is unavoidable with available information.

TABLE 1.—United States fish meal supplies, 1955-76 (thousands of metric tons). (National Marine Fisheries Service 1975, 1977.)

Year	(1) Menhaden	(2) Tuna	(3) Anchovy	(4) Other[1]	(5) Imports	(6) Exports	(7) Total supply protein basis[2]
1955	172.9	21.2	0.0	37.6	88.9	n.a.[3]	195.8
1956	191.1	23.9	0.0	44.1	82.0	n.a.	207.5
1957	156.4	23.3	0.0	51.3	73.7	n.a.	185.3
1958	143.4	23.0	0.0	50.2	91.1	n.a.	188.0
1959	203.1	23.0	0.0	43.1	120.6	n.a.	238.8
1960	198.1	24.0	0.0	33.1	119.4	n.a.	229.6
1961	224.6	19.2	0.0	28.8	197.6	n.a.	291.0
1962	217.5	24.1	0.0	31.5	228.9	n.a.	311.4
1963	167.1	24.5	0.0	33.4	341.4	n.a.	355.7
1964	145.4	19.1	0.0	39.6	398.3	n.a.	380.4
1965	159.7	23.0	0.0	37.3	245.5	n.a.	290.4
1966	122.5	23.0	4.1	42.9	406.2	n.a.	378.6
1967	108.1	23.1	5.1	46.5	591.0	n.a.	492.9
1968	129.9	26.1	2.5	47.4	775.9	n.a.	626.7
1969	144.7	24.4	10.3	42.1	325.1	n.a.	343.6
1970	171.1	24.2	14.7	23.2	227.8	4.3	284.9
1971	200.4	26.6	6.9	22.7	256.9	9.2	314.4
1972	175.6	39.2	10.1	23.8	355.6	9.5	373.2
1973	171.3	39.6	20.0	22.4	62.1	33.3	171.4
1974	185.0	43.7	12.8	23.0	62.0	50.3	167.2
1975	173.6	33.7	25.1	20.9	107.4	10.7	215.0
1976	192.9	36.4	19.9	22.0	127.4	30.0	226.7

[1]Primarily from offal, waste, and scrap from groundfish and herring
[2]Converted to protein as follows: menhaden, exports, and other meal assumed to be 60% protein; anchovy and imports assumed to be 65% protein; tuna meal assumed to be 55% protein. Total supply is production plus imports minus exports.
[3]n.a. means data not available.

TABLE 2.—Annual average prices for various fish meals and average price per unit of protein in fish meal in the United States. (National Marine Fisheries Service 1975.)

Year	(1) Menhaden	(2) Tuna	(3) Domestic anchovy	(4) Peruvian anchovy	(5) Average price per unit protein in fish meal: Actual[1]	(5) Average price per unit protein in fish meal: Deflated[2]
	dollars per metric ton of meal					
1955	123.4	130.7	—	—	1.99	4.34
1956	121.7	121.7	—	—	1.97	4.16
1957	117.7	114.8	—	121.5	1.95	4.01
1958	125.0	124.8	—	128.2	2.01	4.19
1959	116.2	117.1	—	131.9	1.95	3.94
1960	84.4	86.0	—	86.1	1.39	2.80
1961	106.4	99.7	—	100.0	1.69	3.40
1962	112.6	109.5	—	111.2	1.81	3.64
1963	114.1	106.2	—	109.7	1.76	3.58
1964	119.3	115.8	—	119.7	1.88	3.81
1965	152.9	143.2	—	140.3	2.30	4.63
1966	146.1	134.4	137.3	141.9	2.23	4.33
1967	123.8	117.6	117.5	118.1	1.86	3.57
1968	131.8	114.2	110.7	118.8	1.88	3.53
1969	158.1	132.6	137.9	142.5	2.31	4.24
1970	167.4	155.4	156.0	176.4	2.72	4.72
1971	143.3	128.0	140.4	150.7	2.33	3.92
1972	168.3	141.4	154.1	162.6	2.59	4.15
1973	433.8	359.6	365.5	409.8	6.75	9.70
1974	250.5	245.5	270.3	260.6	4.15	4.99
1975	216.9	206.3	214.8	226.5	3.54	3.88
1976	314.3	347.8	247.5	309.9	4.92	5.15

[1]For each meal, price per unit protein equals price per ton divided by percent protein. Average price computed by weighting the price per unit protein for each meal by the proportion of U.S. fish meal protein supplied by that meal.
[2]Deflated by Wholesale Price Index, all commodities (January 1977 = 100).

In addition to the price of fish meal, the demand model should contain independent variables representing 1) the prices of close substitute products, 2) prices of complementary products, and 3) the level of production activity that governs the demand for fish meal. Several high protein meals (e.g., soybean, cottonseed, meat, and bone meals) are potential substitutes for fish meal in poultry rations. Soybean meal is the most common substitute, and its price is used as an independent variable in the demand model. The price of corn meal (Table 3, column 2) is introduced as a complementary product price. Demand for fish meal is expected to increase when the price of a substitute product increases, and is expected to decrease when the price of a complementary product increases. Finally, the overall production of poultry products would cause shifts in the level of demand for fish meal independently of the prices. The poultry and egg production index (Table 3, column 3) is adopted as the appropriate measure of this factor.

In summary, the fish meal demand model is specified as follows:

1) Quantity demanded, the independent variable, is represented by annual production plus net imports of protein-equivalent meal.

2) Annual price of fish meal is measured as the weighted average of the prices per unit protein for all domestically supplied meals.

TABLE 3.—Exogenous variables in the fish meal demand model.

Year	Price of domestic soybean meal[1]	Price of domestic corn[2]	Poultry and egg production index[3] (1976 = 100)
	dollars per metric ton		
1955	51.6	2.24	58
1956	46.5	2.30	63
1957	42.7	2.06	64
1958	50.8	1.99	68
1959	51.3	1.94	70
1960	48.2	1.84	70
1961	57.3	1.80	75
1962	60.3	1.80	75
1963	65.8	2.00	77
1964	62.8	1.99	80
1965	64.9	2.07	83
1966	76.0	2.18	88
1967	69.4	2.06	92
1968	70.3	1.80	90
1969	67.6	1.96	92
1970	71.8	2.19	97
1971	70.7	2.15	98
1972	95.2	2.10	100
1973	216.3	3.57	97
1974	127.8	5.20	97
1975	112.6	4.71	94
1976	147.5	4.37	100

[1]Forty-four percent protein. Simple average price at Decatur, Ill., from National Marine Fisheries Service (1977)
[2]Price of No. 2 yellow corn, Chicago USDA, ERS, Poultry and Egg Situation, PES-294, 1965-77.
[3]From Schultze et al. (1979).

3) Annual domestic price of corn and annual domestic price of soybean meal are introduced as complementary and substitute product prices.
4) The trend in aggregate demand over time is accounted for by the aggregate poultry and egg production in the United States.

All of the variables expressed in dollars are deflated by the Wholesale Price Index to eliminate spurious correlations caused by the inflationary trend.

Functional Form

Demand studies typically utilize least squares regression methodology with either a linear or a log-linear equation. As noted by Chang (1977), however, there is no a priori reason to choose one of these forms. Each form imposes some fairly strict conditions upon the characteristics of the demand function which may contradict theoretical considerations or actual experience. Linear equations imply that the elasticity of demand with respect to any independent variable is a decreasing function of that variable; a log-linear equation implies constant elasticities. Chang suggests that the income elasticity of demand for meat should fall with rising income. A similar consideration applies to fish meal demand. At low prices, feed manufacturers would use near maximum amounts of fish meal allowable and could easily substitute soybean meal for fish meal. With relatively high fish meal prices, feed manufacturers would use a smaller proportion of fish meal, but as price rises further it would be increasingly difficult to maintain desired quantities of lysine and methionine by substitution of soybean meal. Thus it is clearly unwarranted to rule out increasing price elasticity through a priori choice of functional form.

The function to be fitted by regression analysis can be chosen by determining the appropriate transformation of variables for the linear least squares procedure. The log-linear transformation is a special case of a parametric family of transformations introduced by Box and Cox (1964). The parameter defines the transformation

$$x^* = (x^\lambda - 1)/\lambda. \qquad (1)$$

Equation (1) is linear for $\lambda = 1$, and becomes logarithmic as λ approaches zero. The demand function is expressed as

$$q^* = b_0 + b_1 x_1^* + \ldots + b_k x_k^* + u \qquad (2)$$

where q is the quantity demanded, the x's are the independent variables affecting demand, u_t is a stochastic error term, and the b_i and λ are parameters to be determined. The superscript * indicates that the variable has been transformed as in Equation (1).

Price elasticity of demand is defined as the absolute value of the ratio of percentage change in quantity demanded to percentage change in price. Assuming that the first independent variable is the price, $E = \left|\frac{\partial q}{\partial x}\right| \cdot \left(\frac{x_1}{q}\right)$. From Equation (2) we get

$$E = |b_1|(q/x_1)^{-\lambda}. \qquad (3)$$

The elasticity defined in Equation (3) is an increasing function of x_1 when $\lambda > 0$, and is a decreasing function of x_1 when $\lambda < 0$. Thus the estimate of the transformation parameter λ provides a test of whether the price elasticity increases, decreases, or remains fixed along the demand curve.

Simultaneity Bias

In economic theory, the supply and demand curves interact to determine the market price. Over a period of time, shifts in both supply and demand factors cause the market price and observed quantities of products to vary. Without these shifts, only one price and quantity would be observed, making it impossible to estimate a demand or supply curve. When the demand curve remains stable, the observed price-quantity pairs "trace out" the demand curve with, of course, some stochastic error, and a regression analysis will result in a demand curve estimate. When the supply curve remains stable, the observed data will fall along the supply curve, and a regression analysis of the price-quantity relationship results in a supply curve estimate. If shifts in both demand and supply occur, the resulting data will not unambiguously identify either of these two curves, and an ordinary least squares regression will generally result in a set of parameters reflecting neither the supply curve nor the demand

curve. In this case the estimated parameters are said to suffer from simultaneity bias.

The general statistical problems associated with estimation of individual structural relationships in a simultaneous equation system were first examined by Haavelmo (1943). Development of appropriate statistical methods for estimating simultaneous equation systems has been a major area of research for econometricians over the last two decades (Kmenta 1971). In estimating the demand curve for fish meal, however, direct regression estimates seem appropriate, because most of the observed variations in annual fish meal supplies are due to exogeneous shifts rather than price-induced movements along a stable supply curve. Production of fish meal is subject to wide fluctuations due to uncontrolled variations in the fish stocks exploited (Kolhonen 1974). At the same time, formula feed and poultry industries have remained relatively stable during the last 20 yr except for the secular growth accounted for in the analysis. Under conditions in which the random shifts in supply are much greater than the corresponding shifts in demand, the ordinary least squares procedure results in no significant simultaneity bias (Rao and Miller 1971).

Lagged Response Mechanisms

The use of annual price and quantity data for estimating the demand function requires that the response to a change in price occurs rather rapidly, at least within a period of time much shorter than a year. Since most domestic formula feed manufacturers employ professional nutritionists and cost-minimizing computer routines in calculating formulas, the response to changes in the vector of prices is probably rapid. If so, each annual quantity consumed may be assumed to represent at least approximately an equilibrium demand response to the set of independent variables. The assumption of rapid response and equilibrium approximation, however, has not been directly verified. In the interests of rigor it is useful, therefore, to consider alternative assumptions.

A lagged response to a change in price may occur due to rigidities in mixing procedures or personnel, inventory management problems, or time lags in renegotiating contracts for supply of input or sales of products. If any of these factors results in a sluggish response in the substitution between fish meal and other protein meals, the effect of a price change may be drawn out over several periods of time. A fairly simple model for representing a lagged response is the "partial adjustment model" originally developed by Nerlove (1958). Corresponding to any given level of the independent variable, p, there is an optimal or desired level of the dependent variable q. For a demand function with one independent variable, the level of demand fully adjusted to input prices by formula manufacturers represents the desired level of fish meal usage:

$$q_t^d = b\, p_t + u_t \tag{4}$$

where the superscript d signifies desired level.

Because purchasers of meal cannot immediately adjust to this desired level of usage, the demand Equation (4) is not directly observable. By assuming a simple structure to the adjustment process, however, an estimable equation is obtained. The partial model assumes that a fixed percentage of the adjustment to desired level is made each year. This introduces the difference equation

$$q_t - q_{t-1} = \gamma(q_t^d - q_{t-1}). \tag{5}$$

Solving this for q_t and substituting from Equation (4) yields

$$q_t = b\,\gamma\, p_t + (1 - \gamma)q_{t-1} + \gamma u_t. \tag{6}$$

The adjustment parameter, γ, must be a positive number ≤ 1. Larger values of γ imply more rapid adjustment to changes in the independent variable. The impact of a unit change in p_t is distributed over time in an exponentially decaying fashion with successive annual changes in q being equal to $b\gamma$, $b\gamma(1 - \gamma)$, $b\gamma(1 - \gamma)^2$, and so forth. The ultimate change in q due to a change in p is

$$\Delta q = b\Delta p \sum_{j=0}^{\infty} \gamma(1 - \gamma)^j = b\Delta p \tag{7}$$

where j = lag. The elements in the sequence under the summation sign are all positive fractions, and sum to one, so that the sequence can be treated like a probability distribution. Each element represents the percentage of the total effect occuring in year t, and the mean of the distribution, $(1 - \gamma)/\gamma$, represents the mean lag in the adjustment process. Distributed lag models like that in Equation (4) result from other conceptual models such as models of expectations formation

or habit formation. And the exponentially distributed lag is but one of a large class of more complex lag models (Griliches 1967; Kmenta 1971; Rao and Miller 1971).

Application of the partial adjustment model to the demand Equation (2) results in the following:

$$q^*_t = a_0 + \sum_{i=1}^{4} a_i x_i + a_5 q_{t-1} + u_t \qquad (8)$$

where the coefficients a_i can be interpreted in terms of the coefficients of Equation (2) as follows:

$$a_0 = \gamma b_0$$
$$a_i = \gamma b_i;\ i = 1, \ldots 4$$
$$a_5 = (1 - \gamma).$$

STATISTICAL PROCEDURES

For a given value of the transformation parameter, λ, the coefficients of either the equilibrium model [Equation (2)] or the partial Adjustment model [Equation (8)] can be estimated by the ordinary least squares method. Two statistical issues requiring further development, however, are the selection of the "best" value for λ, and the test for significance of the lagged adjustment parameter. An appropriate procedure for estimation of λ was first suggested by Box and Cox (1964). The procedure is more clearly explained in the linear regression context by Kmenta (1971) and is reviewed by Chang (1977). For a fixed value of λ, the linear regression procedure yields an estimate of the error variance $\hat{\sigma}^2$. Box and Cox showed that the maximized log likelihood is, except for a constant,

$$L_{\max}(\lambda) = -(N/2) \log \hat{\sigma}^2(\lambda) + (\lambda - 1)\Sigma \log q_i \qquad (9)$$

A maximum likelihood estimate of λ can, therefore, be found by searching through successive values of λ to maximize Equation (9). The use of this likelihood function implies, of course, that the error terms conform to full normal theory assumptions, i.e., that the u_t are independently normally distributed with zero mean and constant variance. An approximate 100% $(1 - \alpha)$ confidence region for λ is defined by

$$L_{\max}(\hat{\lambda}) - L_{\max}(\lambda) < \tfrac{1}{2}\, \chi_1^2(\alpha) \qquad (10)$$

where $\chi_1^2(\alpha)$ represents the value of the chi-square distribution with 1 df (Box and Cox 1964).

Serial correlation in the errors of the regression model raises problems in the interpretation of the test statistics for the nonlagged variables and the lagged adjustment parameter, and contradicts the assumptions of the log likelihood function. Careful examination of the hypotheses and statistics regarding the residuals of the regression equation is clearly necessary. Existence of serial correlation in the errors of the static demand model can be tested with the Durbin-Watson statistic. If no serial correlation is apparent in the residuals, then neither the distributed lag model nor the serial correlation model need be considered. If serial correlation is present in the residuals of the static model, then the problem is to distinguish between the distributed lag model and the serial correlation model.

Griliches (1967) showed that the serial correlation and lagged adjustment models cannot be distinguished by a simple t-test on the adjustment parameter. For example, if errors generated by a first order Markov process, i.e., $e_t = se_{t-1} + u_t$, occur in a regression equation, the coefficients of the lagged variables may be judged significant by the usual t-test even though there is no real lagged response in the underlying structural relationship. Similarly, it can be shown that serially correlated residuals will occur if a nonlagged model is mistakenly fit to data from an inherently dynamic process.

Although there is no fully satisfactory method for determining which model is the truth, Griliches (1967) developed a provisional test. Briefly, the serial correlation model is

$$q_t = a_0 + \sum_i a_i x_{it} + e_t \qquad (11a)$$

$$e_t = se_{t-1} + u_t \qquad (11b)$$

where s is a positive fraction and u_t is a nonserially correlated error term. From Equation (11a), $e_{t-1} = q_{t-1} - a_0 - \Sigma_i a_i x_{it-1}$; so that $e_t = s(q_{t-1} - a_0 - \Sigma_i a_i x_{it-1}) + u_t$. Substituting this into Equation (11a) yields

$$q_t = (1 - s)a_0 + \sum_i (a_i x_{it} - b_i x_{it-1}) + s\, q_{t-1} + u_t. \qquad (12)$$

When Equation (12) is computed, the serial correlation model implies that $a_i s = -b_i$ for each i. Griliches suggested that the first-order serial correlation model be rejected if these four equalities do not appear to hold. Thus, there are four hypotheses of the following form:

$$H_0: (b_i + sa_i) = 0. \quad (13)$$

An approximate sample variance for $(b_i + sa_i)$ is computed by the "delta method" described by Seber (1973). The expression for approximate variance of a function of a vector of random variables, $G(x)$, is

$$v[G(x)] = \Sigma v(x_i) \left(\frac{\partial G}{\partial x_i}\right)^2 + 2\sum_{i<j}\sum \text{cov}(x_i x_j) \left(\frac{\partial G}{\partial x_i}\right)\left(\frac{\partial G}{\partial x_j}\right). \quad (14)$$

Assuming that the estimate of $(b_i + sa_i)$ from the regression equation is approximately normally distributed, the following ratio will be approximately distributed as an F-statistic with 1 and $(n - r)$ df (where r is the number of regression parameters estimated):

$$(b_i + sa_i)^2/v[b_i + sa_i] \approx F(1, n - r). \quad (15)$$

Since the serial correlation model requires each of the four hypotheses to hold, a definite rejection of one or more of the hypotheses may be taken as evidence against the serial correlation model and in support of the partial adjustment model. Because of the lack of rigor in the suggested testing procedure, however, caution must be exercised in drawing conclusions.

RESULTS

Ordinary least squares estimates of the static demand Equation (2) were computed for a range of values for the transformation parameter λ. The regression coefficients and statistics of most interest are listed in Table 4. A value of $\lambda = -0.55$ maximizes the log likelihood function, but the 95% confidence interval for λ is 0.2 to −1.4. The interval includes the logarithmic transformation ($\lambda = 0$), but not the linear transformation ($\lambda = 1$). The negative value of λ, which implies a price elasticity of demand that decreases as quantity decreases, conforms to expectations. The signs of all the coefficients are also consistent with prior expectations; demand is diminished by increasing price of fish meal or corn meal, and is increased by increasing price of soybean meal and by expanding poultry and egg production. Application of t-tests to the coefficients of the equation with $\lambda = -0.55$ indicates statistical significance with 99% confidence for the coefficients of fish meal price and corn meal price, and with 90% confidence for the coefficient of soybean meal price. The poultry and egg production index appears to be an insignificant influence on fish meal demand by the t-test. But this is insufficient reason for eliminating a theoretically important variable from the equation.

The squared multiple correlation coefficient, $r^2 = 0.73$, indicates a reasonably "good fit" for a demand equation estimate from time-series data.

TABLE 4.—Regressions for determining maximum log-likelihood of static demand function. P_f = price of fish meal, P_s = price of soybean meal, P_c = price of corn feed, Q_p = poultry and egg production index. Superscript * indicates Box-Cox transformation expressed in Equation (1).

Transformation parameter (λ)	Intercept	Coefficient P_f^*	P_s^*	P_c	Q_p^*	R^2	D-W[1]	$L\max(\lambda)$
0.5	44.184	−10.144	9.588	−8.597	0.816	0.695	0.754	−91.21
[2]0.2	12.499	−2.620	2.174	−2.532	0.545	0.714	0.716	−89.70
0.0	6.054	−1.064	0.812	−1.125	0.413	0.722	0.704	−88.97
−0.20	3.324	−0.432	0.305	−0.501	0.311	0.727	0.705	−88.48
−0.50	1.731	−0.112	0.071	−0.150	0.199	0.730	0.725	−88.14
[3]−0.55	1.592	−0.089	0.056	−0.123	0.184	0.730	0.731	−88.13
	(5.108)	(−2.602)	(1.864)	(−3.489)	(0.976)			
−0.60	1.474	−0.071	0.044	−0.100	0.171	0.730	0.735	−88.14
−0.70	1.282	−0.455	0.027	−0.067	0.146	0.729	0.751	−88.18
−1.0	0.929	−0.012	0.007	−0.020	0.088	0.724	0.801	−88.56
−1.2	0.789	−0.005	0.003	−0.009	0.061	0.719	0.839	−89.02
[2]−1.4	0.687	−0.002	0.001	−0.004	0.042	0.711	0.879	−89.61

[1]D-W stands for Durbin-Watson statistic.
[2]Indicates approximate 90% confidence interval for λ.
[3]Indicates maximum likelihood estimate (t-values in parenthesis).

The Durbin-Watson statistic (0.731) is below the lower critical value (d_l = 0.86 for 21 observations and 4 parameter estimates), indicating significant serial correlation in the errors of the demand model. As suggested above, this serial correlation may be caused by incorrect specification of a static model when a dynamic adjustment model would be more appropriate, or it may reflect true serial correlation in the errors which may in turn be due to some other source of misspecification.

Following the suggestion by Griliches (1967), a regression equation with lagged dependent and independent variables was computed (Table 5). The F-statistics for the four hypotheses associated with the serial correlation model range from 0.119 to 6.516. The critical value for each hypothesis (with $P<0.05$ and for 1 and 11 df) is 4.84. Clearly, only one of the four hypotheses, the one associated with the soybean price, can be rejected with great confidence. Even this may be misleading, because the probability of wrongly rejecting at least one of four hypotheses at the 5% level is 0.183[4]. Due to the provisional nature of the test procedure and the inconclusiveness of the result, it is useful to consider both the static and distributed lag models as plausible representations.

The distributed lag model [Equation (8)] was estimated by ordinary least squares for several values of the transformation parameter λ. Regression coefficients and pertinent statistics for the distributed lag model are listed in Table 6. The log-likelihood function is greatest for λ = −0.3, and the approximate 95% confidence interval for λ is −1.0 to 0.22. As in the earlier nonlagged model, the coefficients of the independent variables have the appropriate signs. Since the coefficient of the lagged dependent variable can be interpreted via Equation (5) as one minus the rate of adjustment parameter, the partial adjustment parameter is 0.503. This implies an average lag of slightly less than one. As expected, buyers of fish meal generally adjust to changing conditions and prices within a year.

TABLE 5.—Estimates for demand function parameters with all variables lagged.[1] Transformation parameter, λ, equals −0.55; and all symbols are as explained in Table 4. R^2 = 0.855.

Variable	Estimated coefficient	SE	F-statistic[2]
$P_f^{\dot{}}(t)$	0.07521	0.03208	0.455
$P_f^{\dot{}}(t\text{-}1)$	0.01861	0.03258	
$P_s^{\dot{}}(t)$	0.07498	0.0297	6.516
$P_s^{\dot{}}(t\text{-}1)$	0.03765	0.03609	
$P_c^{\dot{}}(t)$	−0.2059	0.07897	0.119
$P_c^{\dot{}}(t\text{-}1)$	0.1159	0.04239	
$Q_p^{\dot{}}(t)$	1.3352	0.5497	4.006
$Q_p^{\dot{}}(t\text{-}1)$	−1.5422	0.5309	
$q^*(t\text{-}1)$	0.5164	0.1979	—

[1] $q^{\dot{}}(t) \quad a_0 + a_1 P_f^{\dot{}}(t) + b_1 P_f^{\dot{}}(t-1) + a_2 P_s^{\dot{}}(t) + b_2 P_s^{\dot{}}(t-1) + a_3 P_c^{\dot{}}(t) + b_3 P_c^{\dot{}}(t-1) + a_4 Q_p^{\dot{}}(t) + b_4 Q_p^{\dot{}}(t-1) + a_5 q^{\dot{}}(t-1)$

[2] The hypothesis to be tested is $(b_i + a_i a_5) = 0$; and the corresponding F-statistic is $F_i = (b_i + a_i a_5)^2 / \mathrm{Var}(b_i + a_i a_5)$

DISCUSSION

Both the static demand model and the partial adjustment model provide reasonable levels of statistical fit to the historical data series and the signs and magnitudes of the regression

[4] The probability of type 1 error in a single test is 0.05. If four tests are made the probability of making at least one type 1 error is one minus the probability of making no type 1 errors, i.e., $1 - (0.95)^4$.

TABLE 6.—Regression equations for determining maximum log-likelihood of distributed lag form of demand function. P_f = price of fish meal, P_s = price of soybean meal, P_c = price of corn feed, Q_p = poultry and egg production index, q_{t-1} = quantity of fish meal, lagged. Superscript * indicates Box-Cox transformation expressed in Equation (1).

Transformation parameter (λ)	Intercept	Coefficient $P_f^{\dot{}}$	$P_s^{\dot{}}$	$P_c^{\dot{}}$	$Q_p^{\dot{}}$	$q_{t-1}^{\dot{}}$	R^2	$L\max(\lambda)$
1.0	297.904	−103.141	105.367	−21.018	0.694	0.468	0.766	−81.133
0.6	40.639	−16.897	13.097	−3.821	0.537	0.485	0.800	−83.953
0.1	4.122	−1.792	0.902	−0.482	0.389	0.498	0.822	−81.507
0	2.761	−1.147	0.522	−0.323	0.363	0.499	0.824	−81.259
−0.2	1.373	−0.470	0.170	−0.147	0.314	0.498	0.825	−81.014
[1] −0.3	1.030	−0.301	0.098	−0.100	0.291	0.497	0.824	−81.013
	(1.396)	(−3.567)	(1.161)	(−0.840)	(1.189)	(2.907)		
−0.4	0.809	−0.193	0.056	−0.068	0.268	0.494	0.822	−81.090
−0.5	0.665	−0.124	0.031	−0.047	0.247	0.491	0.819	−81.239
−1.0	0.404	−0.013	0.002	−0.008	0.153	0.458	0.795	−82.853

[1] Indicates maximum likelihood estimate (t-values in parentheses).

coefficients satisfy prior expectations. Because it yields a significantly higher r^2, and because the test for serial correlation suggested by Griliches (1967) lends it support, I tend to favor the distributed lag model. But the evidence is not really conclusive. For one thing, the "Griliches test" looks only for first-order serial correlation, and it will probably fail to give correct guidance when more complex residual generating processes are present. Another difficulty is the lower precision of the regression coefficients in the distributed lag model. The importance of this depends upon how the demand function is to be used. In fisheries management applications the most important use of the demand model will be for predicting price effects resulting from changes in annual production.

To compare the two demand models, the equations are transformed to give quantity demanded in natural units (tons of fish meal proteins) and the 1976 values of independent variables other than fish meal price are inserted. The resulting relationships between price and quantity are

TABLE 7.—Demand predictions ($\hat{q}$) and price elasticities (E) for static demand ($\lambda = -0.55$) and partial adjustment ($\lambda = -0.3$) models.

Price of fish meal protein (P_f)	Static demand model		Partial adjustment model	
	$\hat{q}$	E	$\hat{q}$	E
2	852.5	2.49	4,971.0	6.26
4	295.2	0.95	372.3	2.34
6	215.1	0.64	168.8	1.63
8	182.8	0.50	110.7	1.32
10	165.0	0.42	84.2	1.14

for the dynamic demand model. Quantities predicted by Equations (15) and (16) and price elasticities of demand for a range of prices are listed in Table 7. From the Table and Figure 1 it is clear that the two demand models are grossly similar. At low supply levels (less than about 250 t), however, the predicted price responses are greatly different, as are the quantities demanded when prices are low (<$4 per unit protein). Thus, any conclusions reached on the basis of this demand analysis will be sensitive to the specification of the demand function.

$$q_t = \left[-0.00389 + 0.04916\left(\frac{P_f^{-0.55} - 1}{-0.55}\right)\right]^{\frac{1}{-0.55}} \qquad (16)$$

for the static demand model, and

$$q_t = \left[-0.03486 + 0.18001\left(\frac{P_f^{-0.3} - 1}{-0.3}\right)\right]^{\frac{1}{-0.3}} \qquad (17)$$

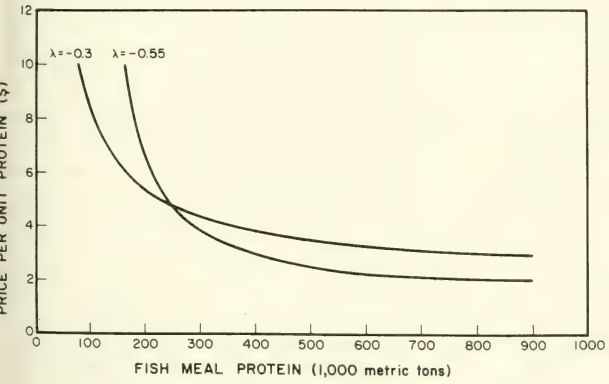


FIGURE 1.—Fish meal demand curves based upon the maximum likelihood estimates of the static demand model ($\lambda = -0.55$) and the partial adjustment model ($\lambda = -0.3$).

Most economic models of fishery management have ignored the influence of landings on the price of fish or fishery products. The assumption of fixed price is a particularly attractive one, because with fixed prices the harvest quantity is proportional to the total revenue. Only the relationship between costs and landings must be added to the model in order to derive economic critertia for optimization. When management programs control landings which are large relative to the market demand, however, the price is likely to become a variable rather than a fixed parameter. The use of demand relationships, such as the one estimated above, will undoubtedly become important as more control is exercised over more fisheries in the United States. The means for incorporating demand analysis into fishery management models is explained by Anderson (1973) and Clark (1976, chapter 5). More extensive use of these complex models which include variable prices will proceed only as fast as the development of solid, empirical demand studies.

ACKNOWLEDGMENTS

I wish to thank Jane McMillan for her extensive assistance in compiling data, managing the computer processing necessary for this paper, and providing professional and computational assistance during the development of our statistical results. Also, I thank James Zweifel for his helpful comments on an earlier draft.

LITERATURE CITED

ANDERSON, L. G.
1973. Optimum economic yield of a fishery given a variable price of output. J. Fish. Res. Board Can. 30:509-518.

BOX, G. E. P., AND D. R. COX.
1964. An analysis of transformations. J. R. Stat. Soc., Ser. B, 26:211-243.

CHANG, H. S.
1977. Functional forms and the demand for meat in the United States. Rev. Econ. Stat. 59:355-359.

CLARK, C. W.
1976. Mathematical bioeconomics: the optimal management of renewable resources. Wiley, N.Y., 352 p.

GRILICHES, Z.
1967. Distributed lags: a survey. Econometrica 35:16-49.

HAAVELMO, T.
1943. The statistical implications of a system of simultaneous equations. Econometrica 11:1-12.

KARRICK, N. L.
1963. Fish meal quality. *In* M. E. Stansby (editor), Industrial fishery technology, p. 253-259. Reinhold Publ. Co., N.Y.

KMENTA, J.
1971. Elements of econometrics. MacMillian Publ. Co., N.Y., 655 p.

KOLHONEN, J.
1974. Fish meal: International market situation and the future. Mar. Fish. Rev. 36(3):36-40.

MEILKE, K. D.
1974. Demand for feed ingredients by U.S. formula feed manufacturers. U.S. Dep. Agric., Agric. Econ. Res. 26:78-89.

NATIONAL MARINE FISHERIES SERVICE.
1975. Industrial fishery products, annual summary 1974. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Curr. Fish. Stat. 6702, 8 p.
1977. Industrial fishery products, market review and outlook. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Curr. Econ. Anal. I-29, 27 p.

NERLOVE, M.
1958. Distributed lags and demand analysis for agricultural and other commodities. U.S. Dep. Agric., Agric. Handb. 141, 121 p.

PACIFIC FISHERY MANAGEMENT COUNCIL.
1978. Northern anchovy fishery management plan. Fed. Regist. 43(141):31655-31783.

RAO, P., AND R. L. MILLER.
1971. Applied econometrics. Wadsworth Publ. Co., Belmont, Calif., 235 p.

SCHULTZ, H.
1938. The theory and measurement of demand. Univ. Chicago Press, Chicago, 817 p.

SHULTZE, C. L., L. E. GRAMLEY, AND W. NORDHAUS.
1979. Annual report of the Council of Economic Advisors. *In* Economic report of the president transmitted to the Congress January 1979, p. 19-306. U.S. Gov. Print. Off., Wash., D.C.

SEBER, G. A. F.
1973. The estimation of animal abundance and related parameters. Hafner Press, N.Y., 506 p.

WAUGH, F. V., AND V. J. NORTON.
1969. Some analysis of fish prices. Univ. R.I. Agric. Exp. Stn. Bull. 401, 68 p.

WOLD, H., AND L. JUREEN.
1953. Demand analysis: a study in econometrics. Wiley, N.Y., 358 p.

WORKING, E. J.
1927. What do statistical "demand curves" show? Q. J. Econ. 41:212-235.

DEVELOPMENT AND STRUCTURE OF FINS AND FIN SUPPORTS IN DOLPHIN FISHES *CORYPHAENA HIPPURUS* AND *CORYPHAENA EQUISELIS* (CORYPHAENIDAE)[1]

THOMAS POTTHOFF[2]

ABSTRACT

The development and structure of the fins and fin supports were studied from a cleared and stained size series of about 400 *Coryphaena hippurus* and about 400 *C. equiselis*. *Coryphaena hippurus* and *C. equiselis* differ in all aspects of fin ray and fin support development; *C. equiselis* is always more advanced than equal-sized *C. hippurus* during development. The species differ in number of fin rays in the single dorsal fin. The pterygiophores of the single dorsal fin each develop from a single cartilage in both species. The cartilage then ossifies to proximal and distal radials. Each fin ray is serially associated with a distal and proximal radial, and each ray is secondarily associated with the following (posterior) proximal radial. Exceptions were found at the anteriormost and posteriormost parts of the dorsal fin. The two species differ only slightly in anal fin ray counts. The pterygiophores of the anal fin are similar in development and structure to those of the dorsal fin. The species do not differ in caudal fin ray counts. The caudal fin rays are supported by some of the bones of the caudal complex, which contains one neural spine, one specialized neural arch, two autogenous haemal spines, one autogenous parhypural bone, five autogenous hypural bones, two paired uroneural bones, and two epural bones. During development, hypurals one and two and hypurals three and four fuse, forming the dorsal and ventral hypural plates. The two epurals fuse into one and the two pairs of uroneurals form one pair. Both species have the same number of pectoral fin rays. In both species, pectoral fin rays are directly supported by the scapula and four radials, and indirectly by the cleithrum and the coracoid. The pectoral suspensorium, which consists of seven bones, connects the pectoral bones to the skull. The posterior process of the coracoid develops as a prominent larval structure that disappears during development. The pelvic fins of both species have one spinous and five soft rays. These fin rays are supported on each side by the pelvic basipterygium. The basipterygium develops in similar fashion to a pterygiophore.

The development and anatomy of the fins and fin supports for *Coryphaena hippurus* and *C. equiselis* have not been described. The purpose of this study was to document the development and anatomy of the fins and fin supports for the family Coryphaenidae and to point up differences in meristic counts and arrangement of fin rays and supporting bones between the two species of *Coryphaena* using cleared and stained material.

No complete study of the fins and fin supports for the two *Coryphaena* species has been done. Studies on the osteology and meristic counts exist without use of cleared and stained material. Jordan and Evermann (1896), Nichols (1909), Gibbs and Collette (1959), Rothschild (1964), Miller and Jorgenson (1973), and Shcherbachev (1973) have published meristic counts for the two species. Clothier (1950) gave the meristic counts and an illustration of the head and the vertebral column for *C. hippurus*. Potthoff (1971), using cleared and stained material, studied meristic counts of *C. equiselis*. Collette et al. (1969) reported the vertebral numbers of the two species, and Gregory (1933) depicted the skull of *C. hippurus* and commented on the phylogenetic relationship of *C. hippurus*. Starks' (1930) description of the pectoral girdle of *C. hippurus* was presented without illustrations.

Many publications deal with the biology (age, growth, reproduction, food) of *Coryphaena* spp., usually *C. hippurus* (Schuck 1951; Williams and Newell 1957; Gibbs and Collette 1959; Kojima 1961, 1963a, b, 1964; Beardsley 1967; Rose and Hassler 1968, 1974; Shcherbachev 1973; Takahashi and Mori 1973). Others document the distribution of *Coryphaena* spp., most often that of *C. hippurus* (Williams 1953; Morrow 1954; Pew 1957; Gibbs and Collette 1959; Kojima 1960, 1964; Tibbo 1962; Shcherbachev 1973; Takahashi and Mori

[1]Contribution No. 80-03M, Southeast Fisheries Center Miami Laboratory, National Marine Fisheries Service, NOAA.

[2]Southeast Fisheries Center Miami Laboratory, National Marine Fisheries Service, NOAA, 75 Virginia Beach Drive, Miami, FL 33149.

Manuscript accepted November 1979.
FISHERY BULLETIN: VOL. 78, NO. 2, 1980.

1973). Mito (1960) described the eggs and hatched larvae of *C. hippurus*, and Gibbs and Collette (1959) described large larvae and juveniles of both *Coryphaena* species. Hassler and Rainville[3] described the rearing techniques for *C. hippurus* from planktonic eggs and the subsequent growth to juveniles. Burnett-Herkes (1974) worked on *C. hippurus* parasites of the gills and mouth.

METHODS

Size series of 400 specimens of each species were cleared and stained by the enzyme method of Taylor (1967). The bones of four adult specimens (two *C. hippurus* and two *C. equiselis*) were prepared by boiling in water and removing the boiled flesh. Almost all specimens had been caught in the west Atlantic, Gulf of Mexico, and the Caribbean. A few specimens were from the mid-Atlantic, the east Atlantic, and the east Pacific.

For each fin and fin support system, a representative size series was chosen for each species from the cleared and stained material (Table 1). Thus, the same specimen did not necessarily contribute to each of the series.

The terms preflexion, flexion, and postflexion refer to the flexion state of the notochord in the caudal region during larval development. They are used to describe and highlight larval stages based on Ahlstrom et al. (1976).

Only cleared and stained specimens were measured. Preserved larvae were usually too distorted for accurate measurements, but were easily straightened and measured after clearing and staining. Measurements were to the nearest 0.1 of a millimeter using a calibrated ocular micrometer for the smaller specimens (< 20 mm SL) and dial calipers for the larger ones. Each measurement was either notochord length (NL, from the anterior tip of the upper jaw to the posteriormost tip of the notochord) for preflexion and early flexion larvae, or standard length (SL, from the anterior tip of the upper jaw to the posteriormost edge of the hypural bones) for late flexion and postflexion larvae, juveniles, and adults.

All specimens were examined in 100% glycerin under a binocular microscope, and illustrations were drawn with the help of a camera lucida. Ossification was determined from the uptake of alizarin. Very light uptake (pink) of alizarin in a structure was considered as onset of ossification. Cartilage was determined by the presence of structure but absence of red stain, and viewed by carefully manipulating the illumination with the substage mirror. Specimens from which organic calcium had leached due to acid Formalin[4] did not stain and were not used.

The caudal complex terminologies follow Gosline (1961a, b), Nybelin (1963), and Monod (1968).

Counts of pterygiophores and fin rays include very small and vestigial structures such as fin rays that consisted only of a left or right half, or of two pieces not joined at the center.

[3]Hassler, W. W., and R. P. Rainville. 1975. Techniques for hatching and rearing dolphin, *Coryphaena hippurus*, through larvae and juvenile stages. Univ. N.C., Sea Grant Program UNC-SG-75-31, 17 p.

TABLE 1.—Number and length range (in millimeters NL or SL) of cleared and stained specimens of *Coryphaena* spp. used for study of individual fins and their support structures.

Item	*C. hippurus*		*C. equiselis*	
	No.	Length	No.	Length
Dorsal fin	211	5.0-172	161	6.5-230
Pterygiophores	216	5.0-176	197	6.5-230, 314
Anal fin	212	5.0-172	157	6.5-230
Pterygiophores	216	5.0-176	197	6.5-230, 314
Caudal fin	201	5.0-172	138	6.5-230
Caudal complex	47	5.0-172, 690	45	6.5-230, 330
Pectoral fin and supports	123	5.0-172	164	6.5-230
Pelvic fin and supports	105	6.0-176, 449, 920	76	7.0-172, 315, 330

RESULTS

Vertebral Column

The development and structure of the vertebral column was not examined in this study. However, it was noted that development is similar in all respects for the two *Coryphaena* species as it was reported for *Thunnus atlanticus* (Potthoff 1975).

Neural and haemal spines developed from cartilage before pterygiophores, but were difficult to count accurately. In small specimens (5.9-6.3 mm NL) interneural and interhaemal space numbers were estimated from myomere counts.

Dorsal Fin

The fully developed dorsal fin of *C. hippurus* has 58-66 rays (N = 99, $\bar{x}$ = 61.3, SE = 0.17, 24-172 mm SL) and that of *C. equiselis* 52-59 rays (N = 113, $\bar{x}$ = 55.0, SE = 0.15, 18-230 mm SL). Adult counts for *C. hippurus* are obtained be-

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

tween 18 and 24 mm SL and for *C. equiselis* between 13 and 18 mm SL (Figure 1). Gibbs and Collette (1959) reported 46-65 ($\bar{x}$ = 58.4) dorsal fin rays for *C. hippurus* and 48-60 ($\bar{x}$ = 52.6) for *C. equiselis*. My counts and those of Gibbs and Collette (1959) differ because Gibbs and Collette included counts of small specimens (from about 12 mm SL) of both species in their sample and because *C. equiselis* develops a full complement of dorsal fin rays at a smaller size than *C. hippurus* (13-17 mm SL vs. 18-23 mm SL); therefore, more *C. hippurus* than *C. equiselis* with incomplete dorsal fins were counted by Gibbs and Collette, and inclusion of incomplete dorsal fin ray counts widened the range of counts and lowered the mean number of dorsal fin rays. Dorsal fin ray counts reported by Shcherbachev (1973) (46-67 for *C. hippurus* and 48-60 for *C. equiselis*) are from his own data and those of Gibbs and Collette. Rothschild (1964) reported 54-58 ($\bar{x}$ = 57.9) for adult *C. equiselis*, all from the Pacific Ocean. Here, count differences probably resulted from the method of counting (cleared and stained vs. preserved material) but may also have been due to population differences.

Dorsal fin rays were first seen in *C. hippurus* at 6 mm SL and were present in all specimens at 8 mm SL (Figure 1). The smallest specimen of *C. equiselis* (6.5 mm SL) already had 12 dorsal fin rays. Development of the dorsal fin rays for both species started in the dorsal finfold at the posterior third of the body (Figure 2). This was above the 22d-24th myomere for three *C. hippurus* with only 3 or 4 dorsal fin rays. With growth, addition of dorsal fin rays was in an anterior and posterior direction for both species, but more fin rays were added anteriorly (Figure 2). The dorsal fin, despite the more rapid addition of rays anteriorly, reached completion posteriorly at a smaller size of the larvae than anteriorly. This is because more

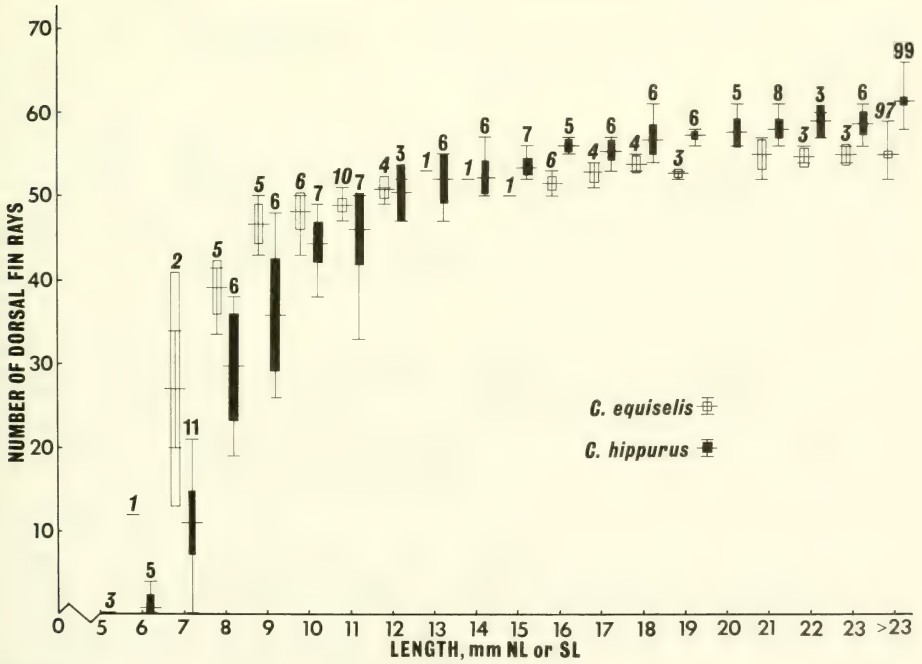
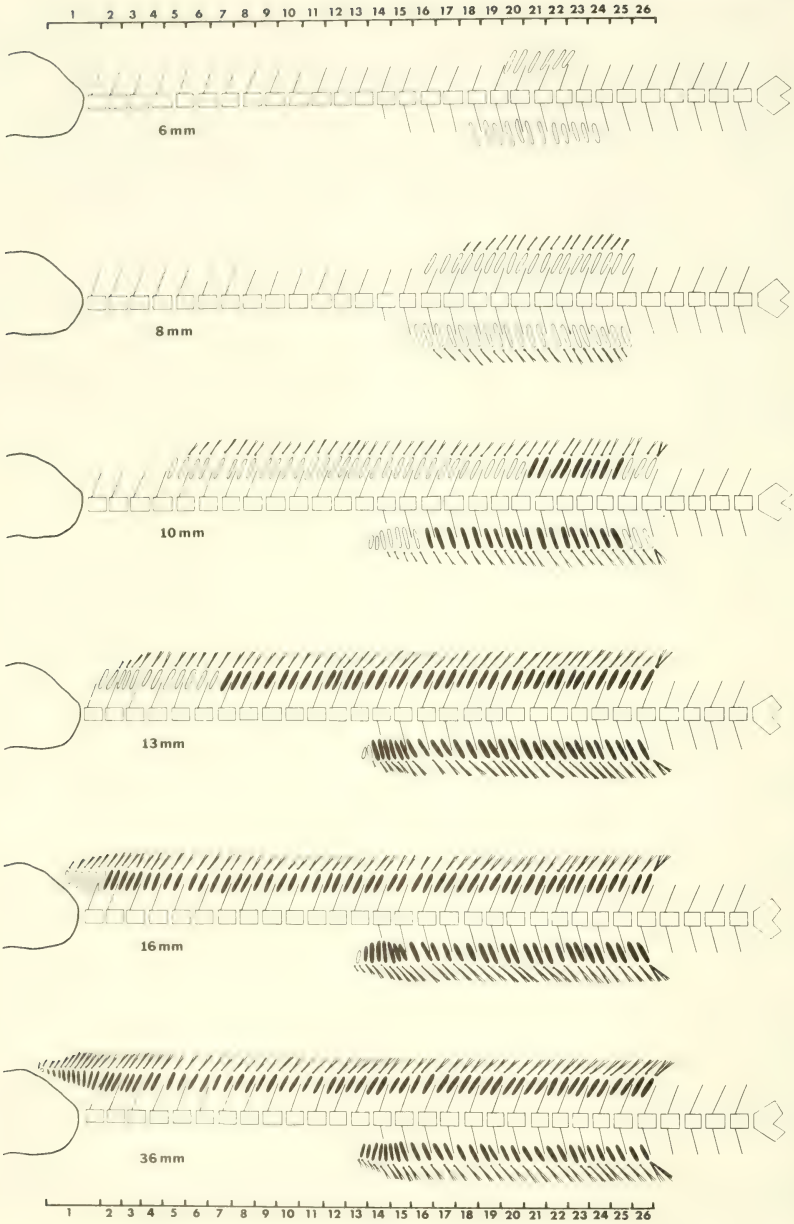


FIGURE 1.—Number of dorsal fin rays in relation to length in 161 *Coryphaena equiselis* (6.5-230 mm NL or SL) and 211 *C. hippurus* (5.0-172 mm NL or SL). Range (vertical line), mean (horizontal line), and 2 standard errors about the mean (white and black bars) are indicated. Number of specimens for each length interval is given above the range and is in italics for *C. equiselis*.


1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26
6 mm
8 mm
10 mm
13 mm
16 mm
36 mm
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26

pterygiophores had to be added from place of origin anteriorly than posteriorly. Small *C. hippurus* (5 mm NL-11 mm SL) usually had fewer fin rays compared to equal-sized *C. equiselis* (Figure 1). Between 12 and 14 mm SL both species had about equal dorsal fin ray numbers. Specimens of *C. hippurus* 15 mm SL and longer usually had more dorsal fin rays than equal-sized *C. equiselis*.

The developmental sequence of dorsal fin rays in *Coryphaena* spp. is similar to that observed in *Trachurus symmetricus* (Ahlstrom and Ball 1954), *Haemulon plumieri* (Saksena and Richards 1975), and *Archosargus rhomboidalis* (Houde and Potthoff 1976). It is as though *Coryphaena* spp. is developing two dorsal fins in the same pattern of the above examples, e.g., first the second dorsal fin followed by the first dorsal. It is of interest to note that most scombroids do not follow this pattern and develop the first dorsal fin first (Voss 1954; Potthoff 1975).

Dorsal Fin Pterygiophores

Counts

There was a supporting pterygiophore in both species of *Coryphaena* in a jointed series for each dorsal fin ray, except for the first two or three anteriormost rays. Each pterygiophore had a proximal and a distal radial. The distal radial was located between the bifurcate base of the fin ray. Proximal and distal radial and fin ray formed a series, hence, a serial association. Each fin ray also closely approximated the following posterior pterygiophore in a secondary association. Thus, each pterygiophore supported a ray in a serial association and an immediately anterior ray in a secondary association. The exceptions were found at the beginning and the end of the fin. The anteriormost pterygiophore supported from one to three rays, but most often two rays (Table 2). Also, in 2 out of 70 specimens of both species, no rays were associated with the anteriormost pterygiophore, and the pterygiophore was very small and almost a vestige. The posteriormost ray in the dorsal fin was a double ray which was serially associated with the posteriormost pterygiophore. This was the only ray in the dorsal fin which lacked a secondary association. Total dorsal fin ray count in both species was either one less than the pterygiophore count, equal to the pterygiophore count, or one or two greater than the pterygiophore count. Thus, the two species differed in their pterygiophore number as they differed in their fin ray counts.

TABLE 2.—Number (adult count) of anteriormost dorsal fin rays without distal radials and number of dorsal fin rays associated with the anteriormost dorsal fin pterygiophore for 28 *Coryphaena hippurus* (78.8-176 mm SL) and 35 *C. equiselis* (74.1-172, 314 mm SL).

Item	Species	Number of anteriormost dorsal fin rays			
		0	1	2	3
Without distal radials	*C. hippurus*		12	12	4
	C. equiselis	1	6	25	4
Associated with the anteriormost pterygiophore	*C. hippurus*		3	24	1
	C. equiselis		1	17	19

In larvae, juveniles and small-sized adults of *Coryphaena* spp. the proximal radials of the dorsal fin were inserted in interneural spaces. The first interneural space was bounded anteriorly by the head and posteriorly by the first neural spine, followed posteriorly by the remaining interneural spaces which were bounded by all other neural spines (Figure 3).

Fully developed specimens of the two species of *Coryphaena* differed by the number of pterygiophores that occupied the interneural spaces. The number of pterygiophores found in the first interneural space separated the species most of the time, with 10-14 ($\bar{x}$ = 11.0) for *C. hippurus* and 7-11 ($\bar{x}$ = 8.0) for *C. equiselis* (Figures 3, 4). The species also differed in the number of pterygiophores associated with the remainder of the interneural spaces. Although individual variability within each interneural space was too great to allow this character to be used to separate the species, the mean number of pterygiophores in each interneural space was always greater for *C. hippurus*.

The species also differed in the number of interneural spaces that were occupied by the dorsal fin pterygiophores (Figure 3; Tables 3, 4). In *C. hippurus* the dorsal fin pterygiophores extended to the 26th interneural space and seldom to the 27th, whereas in *C. equiselis* they extended to the 28th and seldom to the 27th or 29th space. There was some overlap for the two species in this character, but if the termination of the anal fin pterygiophores was taken into account, together

FIGURE 2.—Schematic representation of dorsal and anal fin and pterygiophore development in *Coryphaena hippurus* in relation to the vertebral column and head. Oval-shaped representation of pterygiophores are cartilaginous when white and ossifying when black. Scale represents interneural and interhaemal spaces and points align with midpoint of vertebral centra.

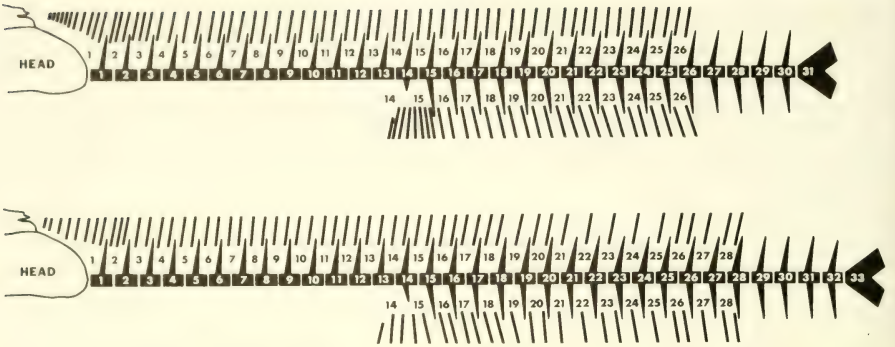


FIGURE 3.—Schematic representation of the relationship of dorsal and anal fin pterygiophores to the vertebral column in adult *Coryphaena hippurus* (upper) and *C. equiselis* (lower). Black numbers, interneural and interhaemal spaces; white numbers, centra.

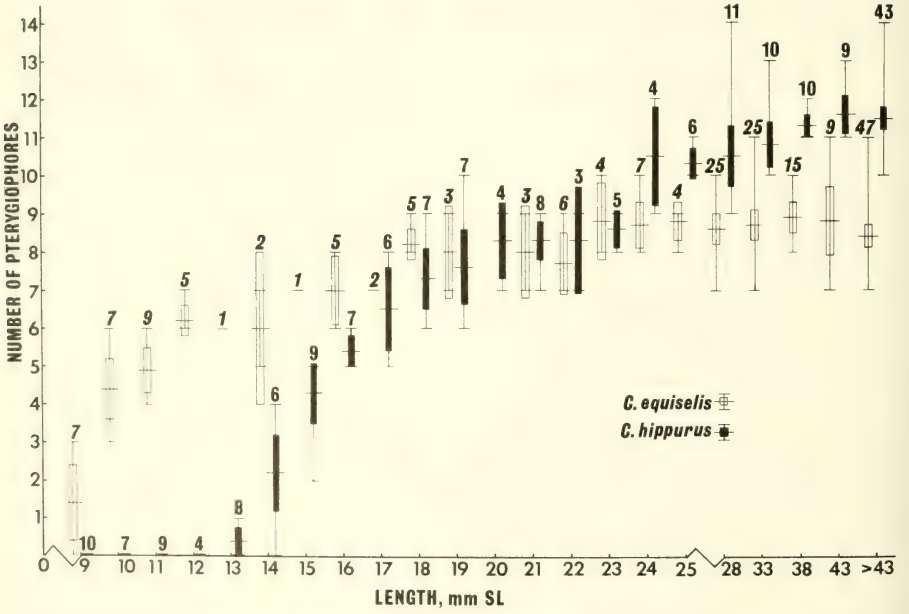


FIGURE 4.—Number of pterygiophores in the first interneural space in relation to length in 192 *Coryphaena equiselis* (8.6-173, 314 mm SL) and 193 *C. hippurus* (8.6-176 mm SL). For explanation of symbols, see Figure 1.

with the termination of the dorsal fin pterygiophores, complete separation for the two species resulted (Figure 3, Table 3).

Dorsal fin pterygiophores had the same pattern of appearance in both species of *Coryphaena* as the dorsal fin rays. Cartilaginous pterygiophores

TABLE 3.—Adult and juvenile position of posteriormost dorsal and anal fin pterygiophores in their interneural and interhaemal spaces for 193 *Coryphaena hippurus* (9.0-176 mm SL) and 186 *C. equiselis* (8.9-172, 314 mm SL). For numbering of vertebrae and spaces, see Figure 3.

	Interneural space numbers / Interhaemal space numbers										
Species	26/25	26/26	26/27	27/26	27/27	27/28	28/28	28/27	28/28	28/29	29/28	29/29
C. hippurus	2	172	3	11	5							
C. equiselis						2	2	172	1	4	5	

without rays were first seen in the 22d-24th myomeres at 5.9 mm NL in *C. hippurus* (Figure 2) and with some rays in the 18th-27th myomeres at 6.5 mm NL in the smallest available but more advanced *C. equiselis*. In both species of *Coryphaena* the pterygiophores appeared shortly before the fin rays developed. As pterygiophores were added, anteriorly and posteriorly rays were lacking for one or two anteriormost and posteriormost additions (Figure 2).

In both species, the posteriormost interneural spaces (numbers 26-28) were occupied with pterygiophores between 7 and 8.5 mm SL (Table 4). The anteriormost interneural space started to fill with pterygiophores at 9.3 mm SL in *C. equiselis* and at 13.1 mm SL in *C. hippurus* (Figure 4, Table 4). Adult counts in the anteriormost interneural space of 7-11 pterygiophores were obtained for *C. equiselis* between 12.3 and 23.2 mm SL and for *C. hippurus* of 10-14 pterygiophores between 18.7 and 30.8 mm SL (Figure 4, Table 4).

Ossification of the pterygiophores started in the same area and proceeded in the same directions as the cartilaginous development (Figure 2). Ossification of pterygiophores occurred first at 8.8 mm SL in *C. equiselis* and at 9.7 mm SL in *C. hippurus* (Table 4). The posteriormost interneural space number 28 of *C. equiselis* had ossifying pterygiophores at 8.9 mm SL, and posteriormost interneural space number 26 of *C. hippurus* had ossifying pterygiophores at 10.2 mm SL (Table 4). Specimens 10.3-11.6 mm SL of *C. equiselis*, and 16.2-19.2 mm SL specimens of *C. hippurus* had one or more ossifying pterygiophores in the first interneural space (Figure 4, Table 5). All dorsal fin pterygiophores were ossifying in both species at about 45 mm SL when the count of ossifying pterygiophores was in the adult range and the first interneural space did not have anterior cartilaginous pterygiophores (Figures 4, 5).

TABLE 4.—Development of dorsal fin pterygiophores in the interneural spaces for 105 *Coryphaena hippurus* and 53 *C. equiselis*. For numbering interneural spaces, see Figure 3.

Length mm NL or SL	Interneural space numbers with pterygiophores				Interneural space numbers with ossifying pterygiophores				Number of specimens	
	Anteriormost space no. (*x*)		Posteriormost space no. (*x*)		Anteriormost space no. (*x*)		Posteriormost space no. (*x*)			
	C. hippurus	*C. equiselis*	*C. hippurus*	*C. equiselis*	*C. hippurus*	*C. equiselis*	*C. hippurus*	*C. equiselis*	*C. hippurus*	*C. equiselis*
4.5- 5.5	[1])	—	[1])	—	([2])	—	([2])	—	1	—
5.6- 6.5	19-22(20.3)	18	22-25(23.3)	27	([2])	([2])	([2])	([2])	3	1
6.6- 7.5	[1]6-22(17.7)	15	[1]23-27(25.2)	28	([2])	([2])	([2])	([2])	9	1
7.6- 8.5	8-16(12.6)	5-10(7.0)	25-26(25.6)	28	([2])	([2])	([2])	([2])	3	4
8.6- 9.5	5-13(11.5)	1- 3(1.6)	26	28	([2])	[2]4-23(12.0)	([2])	[2]25-28(27.2)	10	7
9.6-10.5	2- 6(3.7)	1	26	28	[2]13-21(16.6)	1- 6(3.4)	[2]25-26(25.8)	28	7	7
10.6-11.5	2- 7(3.2)	1	26	28	[2]11-18(15.1)	1- 2(1.7)	[2]25-26(25.9)	28	9	9
11.6-12.5	2	1	26	28-29(28.2)	9-16(12.0)	1	26	28-29(28.2)	4	5
12.6-13.5	1- 2(1.6)	1	26-27(26.1)	28	4-11(7.7)	1	26-27(26.1)	28	8	1
13.6-14.5	1- 2(1.1)	1	26-27(26.1)	28	3- 9(4.3)	1	26-27(26.1)	28	9	1
14.6-15.5	1	1	26-27(26.4)	28	2- 4(2.8)	1	26-27(26.4)	28	10	1
15.6-16.5	1	1	26-27(26.1)	28	1- 3(2.0)	1	26-27(26.1)	28	7	5
16.6-17.5	1	1	26	28-29(28.3)	1- 2(1.3)	1	26	28-29(28.3)	7	3
17.6-18.5	1	1	26-27(26.1)	28	1	1	26-27(26.1)	28	7	5
18.6-19.5	1	1	26-27(26.1)	28	1- 2(1.1)	1	26-27(26.1)	28	7	3
19.6-20.5	1	—	26	—	1	—	26	—	4	—

[1]No pterygiophores developed.
[2]No pterygiophores ossified

TABLE 5.—Sum (adult count) of anal fin pterygiophores in the two anteriormost interhaemal spaces, numbers 14 and 15, in 35 *Coryphaena hippurus* (49.9-176 mm SL) and 32 *C. equiselis* (74.1-172, 314 mm SL). For numbering interhaemal spaces, see Figure 3.

	Number of pterygiophores						
Species	4	5	6	7	8	9	10
C. hippurus				14	18	2	1
C. equiselis	5	20	6	1			

Morphology and Development

The pterygiophores in the center area of the dorsal fin developed first in both species. A pterygiophore (proximal and distal radial) appeared as one elongate piece of cartilage (Figure 6). Ossification was first observed at the middle part of the pterygiophore cartilage (Figure 6) and proceeded distally and proximally along the cartilage until only cartilage tips were present at the extremities. At this point, the sagittal and lateral keels began to develop (Figure 4). Further development of the pterygiophore consisted of growth of the keels, growth of bone around the locus of secondary fin ray association, and segregation and ossification of the distal radial. The distal radial developed from the distal tip of the pterygiophore cartilage late during ontogeny (Figure 6), and ossified into two pieces of bone (Figure 7).

The pterygiophores in the posteriormost area of the dorsal fin developed similarly to those of the center area. The posteriormost pterygiophore supported one ray in series. This ray developed from two rays but was counted as one according to Hubbs and Lagler (1958). In adults, the base of the anterior ray fitted closely over the base of the posterior ray and the base of the posterior ray articulated with the distal radial of the posteriormost pterygiophore (Figures 8, 9).

The supports of the anterior portion of the dorsal fin developed last. In *C. equiselis* the first interneural space was almost filled with cartilaginous pterygiophores, but in equal-sized *C. hippurus* the first interneural space was empty and the second interneural space had only one cartilaginous pterygiophore (Figures 10, 11). The anteriormost cartilaginous pterygiophores always had

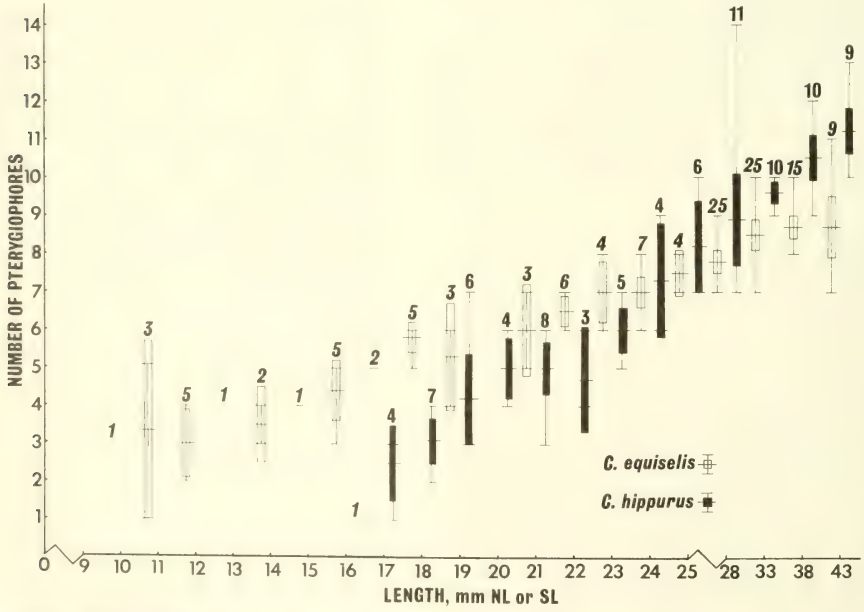


FIGURE 5.—Number of ossifying pterygiophores in the first interneural space in relation to length in 126 *Coryphaena equiselis* and 88 *C. hippurus*. For explanation of symbols see Figure 1.

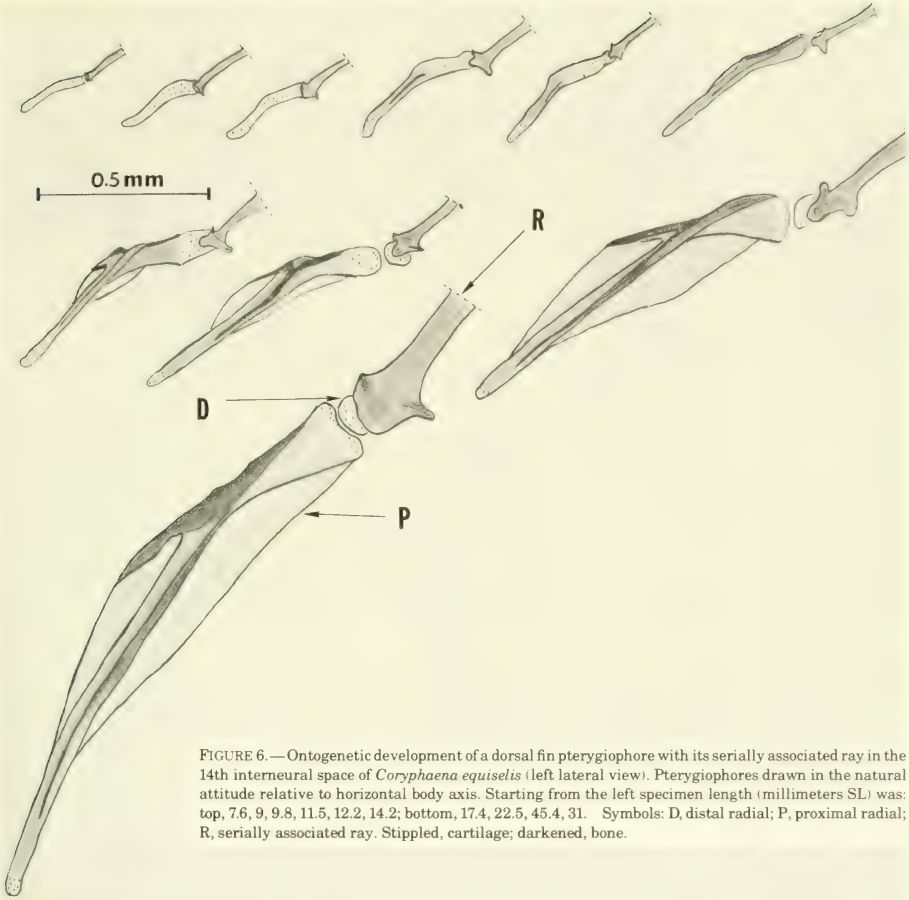


FIGURE 6.—Ontogenetic development of a dorsal fin pterygiophore with its serially associated ray in the 14th interneural space of *Coryphaena equiselis* (left lateral view). Pterygiophores drawn in the natural attitude relative to horizontal body axis. Starting from the left specimen length (millimeters SL) was: top, 7.6, 9, 9.8, 11.5, 12.2, 14.2; bottom, 17.4, 22.5, 45.4, 31. Symbols: D, distal radial; P, proximal radial; R, serially associated ray. Stippled, cartilage; darkened, bone.

a ray developing concurrently (Figures 2, 10, 11). In specimens of both species, which had the full count of pterygiophores in the first interneural space, it was common to have a ray develop in front of the cartilaginous pterygiophore (Figure 2). The pterygiophores of the first interneural space in large juveniles and adults of both species were vertical to the body axis near the first neural spine and slightly anteriorly inclined dorsad near the head (Figure 12). The anteriormost pterygiophore in the adults was either of normal size (not figured), very small (Figures 12, 13), or just a vestige (not figured). In a few instances, in both species, the anteriormost pterygiophore was completely or partially fused to the second pterygiophore. The anteriormost pterygiophore of both species had either one, two, or three associated rays (Table 2). For the two species the anteriormost dorsal fin ray was either normal in size or a vestige (Figures 12, 13). In both species three types of first fin ray vestiges were observed: a paired vestige (Figure 13), a single right vestige, and a single left vestige.

Distal radials were present between the bases of each fin ray for almost the entire dorsal fin. Distal radials were last to ossify from the distal portion of the pterygiophore cartilage. Only the anteriormost three fin rays of both species sometimes

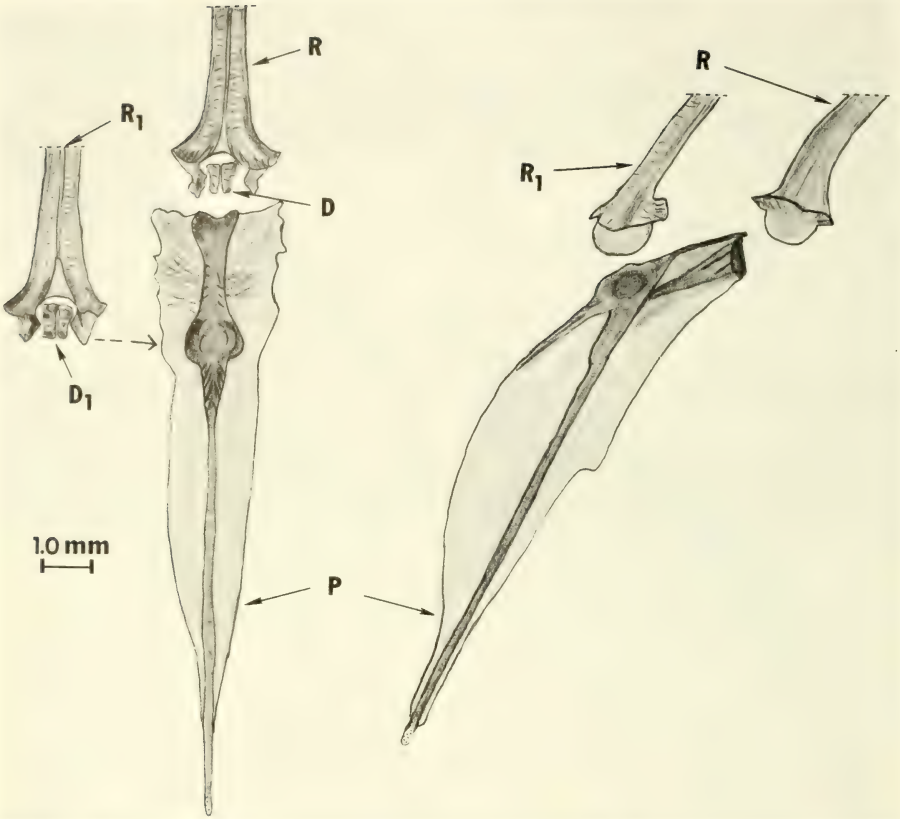


FIGURE 7.—Pterygiophore from 14th interneural space with its secondarily and serially associated rays from a 230 mm SL *Coryphaena equiselis*. Left: anterodorsal view, secondarily associated ray moved to the right of the proximal radial; right: left lateral view. Symbols: D_1, distal radial of secondarily associated ray; D, distal radial of serially associated ray; P, proximal radial; R_1, secondarily associated ray; R, serially associated ray. Stippled, cartilage; darkened, bone.

lacked distal radials. The absence or presence of distal radials was not related to the number of fin rays associated with the anteriormost pterygiophore (Table 2). The first three or four (anteriormost) distal radials of both species differed in structure from the remainder. These radials consisted of one piece of bone (Figure 14) whereas all other radials were of two pieces (Figures 7, 8).

The dorsal pterygiophores of *Coryphaena* spp. differed in several ways from other perciform fishes. Predorsal bones reported in Apogonidae (Fraser 1972), Serranidae and Grammistidae (Kendall 1976), Sparidae (Houde and Potthoff 1976), and for all the stromateoid families (Ahlstrom et al. 1976) were lacking. Also lacking was the terminal bone in the dorsal fin support series called a "stay" by Weitzman (1962). Stays have been reported for such families as Characidae (Weitzman 1962), Scombridae (Kramer 1960; Potthoff 1975), Sparidae (Houde and Potthoff 1976), Nomeidae and Centrolophidae (Ahlstrom et al. 1976), and Centropomidae, Kyphosidae, Lutjanidae, Percichthyidae, and Scorpidae (Johnson 1978). A stay was observed in the Scombrolabracidae and a double stay in the Gempylidae (Potthoff et al. 1980).

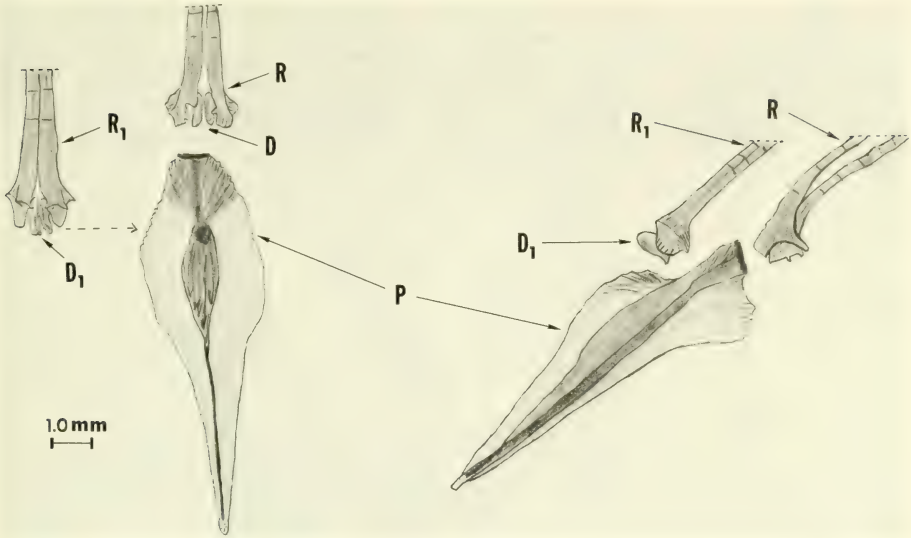


FIGURE 8.—Posteriormost dorsal fin pterygiophore with its secondarily and serially associated rays from a 230 mm SL *Coryphaena equiselis*. Left: anterodorsal view, secondarily associated ray has been moved to the right of the proximal radial; right: left lateral view, pterygiophore has been tilted 30° from the horizontal toward the vertical. Symbols: D_1, distal radial of secondarily associated ray; D, distal radial of serially associated double ray; P, proximal radial; R_1, secondarily associated ray; R, serially associated double ray. Stippled, cartilage; darkened, bone.

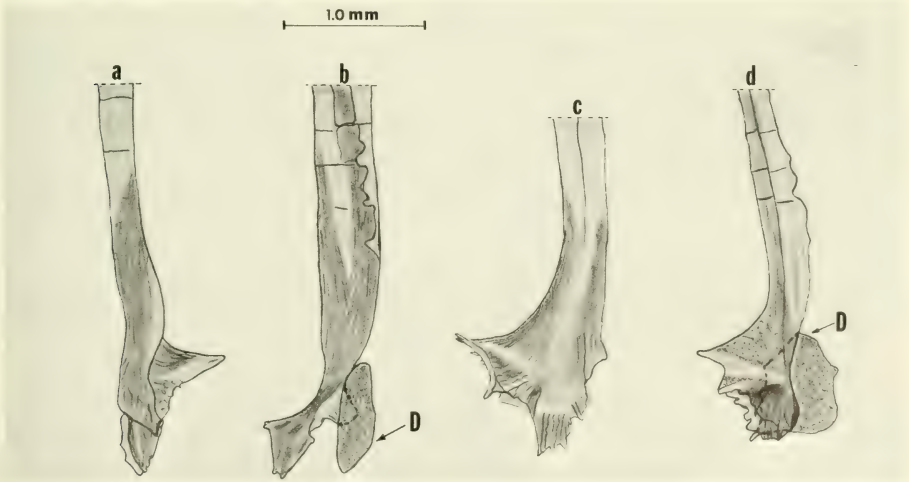


FIGURE 9.—Anterior and right lateral views of right side of a disarticulated posteriormost double dorsal fin ray with its distal radial from a 230 mm SL *Coryphaena equiselis*. a, right half of anterior ray, anterior view; b, right half of posterior ray and right half of its distal radial, anterior view; c, right half of anterior ray, lateral view; d, right half of posterior ray and right half of its distal radial, lateral view. Symbol: D, distal radial.

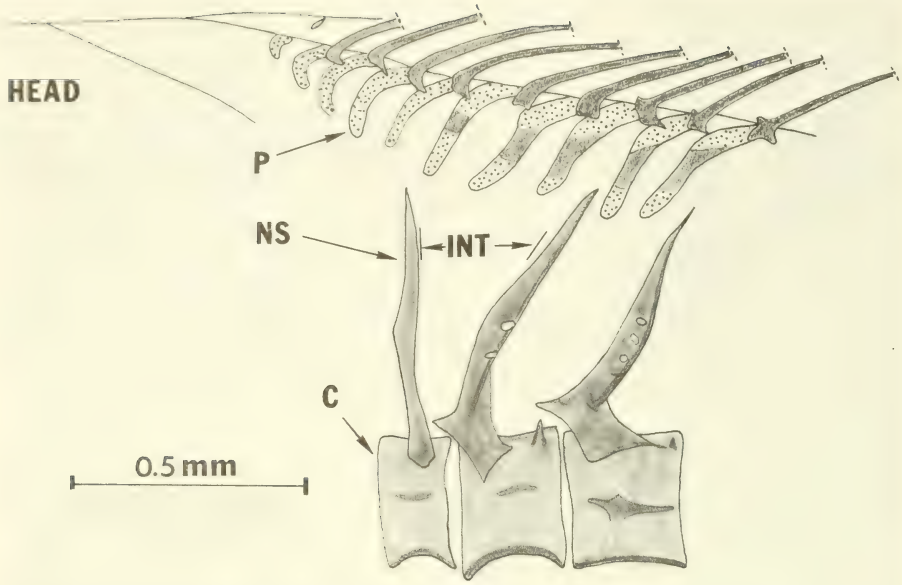


FIGURE 10.—Left lateral view of anteriormost part of the dorsal fin and pterygiophores for a 11 mm SL *Coryphaena equiselis*, showing relationship of pterygiophores to head, interneural spaces, and centra. Symbols: C, first centrum; INT, second interneural space; NS, first neural spine; P, proximal radial. Stippled, cartilage; darkened, bone.

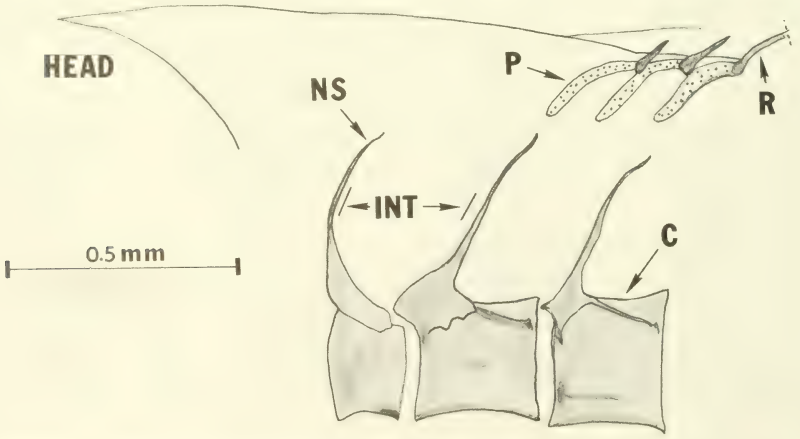


FIGURE 11.—Left lateral view of anteriormost part of the dorsal fin and pterygiophores for a 11 mm SL *Coryphaena hippurus*, showing the relationship of pterygiophores to head, interneural spaces, and centra. Symbols: C, third centrum; R, dorsal fin ray. For explanation of other symbols, see Figure 10. Stippled, cartilage; darkened, bone.

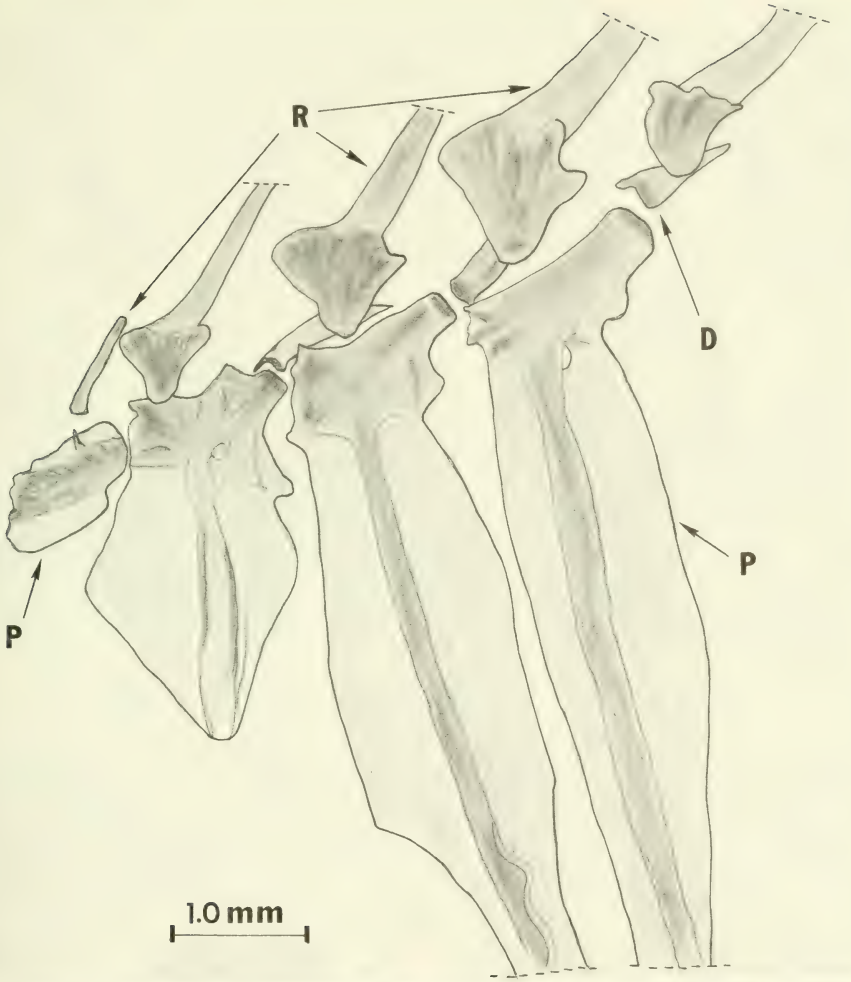


FIGURE 12.—Left lateral view of four anteriormost dorsal fin pterygiophores with secondarily and serially associated rays from a 230 mm SL *Coryphaena equiselis*. Symbols: R, dorsal fin ray; P, proximal radial; D, distal radial.

The proximal and distal radials (except the anteriormost three or four) of *Coryphaena* spp. were similar along the entire fin and were located between the bifurcate bases of the fin rays. Middle radials were absent in the posterior portion of the fin. In most other perciform fishes, distal radials differ between the first and second dorsal fins. The first dorsal fin distal radials are anterior to the bases of the fin spines, and the second dorsal fin distal radials are between the bifurcate bases of the fin rays, and middle radials are present posteriorly. Anatomically different distal radials for the first and second dorsal fins and the presence of middle radials posteriorly have been reported in the Carangidae (Berry 1969), Scombridae (Kramer 1960; Potthoff 1974, 1975),

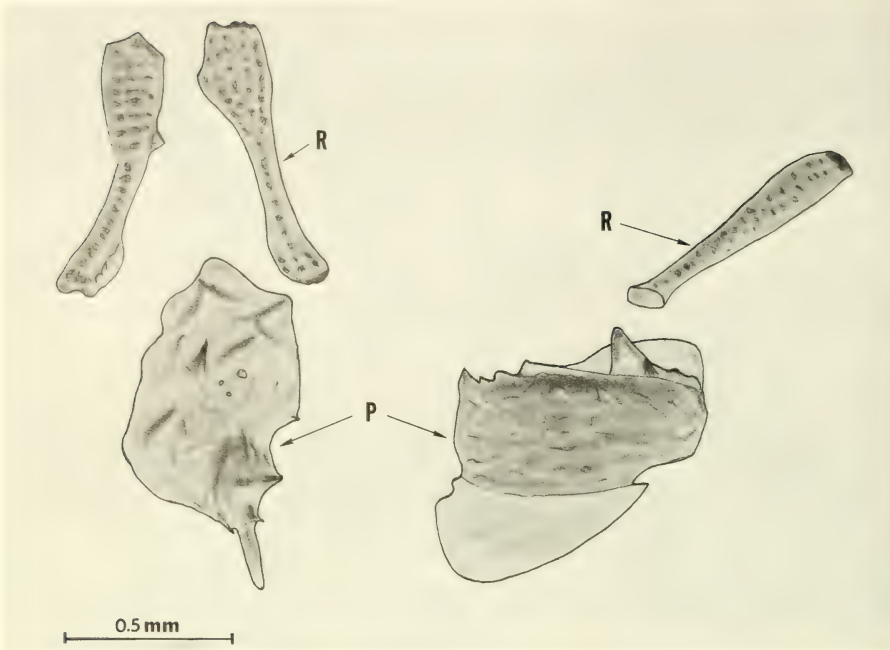


FIGURE 13.—Anteriormost dorsal fin pterygiophore with secondarily associated vestigial ray from a 230 mm SL *Coryphaena equiselis*. Left: anterodorsal view, right: left lateral view. Symbols: P, proximal radial; R, vestigial ray.

Sparidae (Houde and Potthoff 1976), Centropomidae, Kyphosidae, Lutjanidae, Percichthyidae, and Scorpidae (Johnson 1978), and Gempylidae and Scombrolabracidae (Potthoff et al. 1980).

Anal Fin

The fully developed anal fin of *Coryphaena hippurus* has 25-31 rays (N = 147, $\bar{x}$ = 28, SE = 0.01, 16-172 mm SL) and that of *C. equiselis* 23-29 (N = 118, $\bar{x}$ = 26, SE = 0.01, 16-230 mm SL). The anal fin ray counts, in contrast to the dorsal fin ray counts, differ only slightly from those reported by Gibbs and Collette (1959), Rothschild (1964), and Shcherbachev (1973). Both species have adult anal fin ray counts at smaller sizes than dorsal fin ray counts (*C. hippurus* at 8-11 mm SL, *C. equiselis* at 8-9 mm SL).

Anal fin rays were first seen in some *C. hippurus* at 6 mm NL, just before the onset of dorsal fin ray development and all *C. hippurus* had anal rays at 7 mm NL (Figure 15). The smallest available (6.5 mm NL) *C. equiselis* had 14 anal rays. Development of the anal fin of both species began in the finfold at the approximate center of the fin, below the 22d or 23d myomere. Addition of rays was in an anterior and posterior direction for both species (Figure 2). As in the dorsal fin, the posterior portion of the anal fin was completed first and the anteriormost rays developed last. From 6 mm NL to 9 mm SL, *C. hippurus* had fewer anal fin rays than *C. equiselis*; at 10 and 11 mm SL, both species had about equal numbers of rays; at 12 mm SL and longer, *C. hippurus* tended to have more anal rays than *C. equiselis* (Figure 15).

Appearance and additional sequence of anal fin rays in *Coryphaena* spp. are similar to *Scomber japonicus* (*Pneumatophorus diego*) (Kramer 1960), *Thunnus atlanticus* (Potthoff 1975), *Haemulon plumieri* (Saksena and Richards 1975), and *Archosargus rhomboidalis* (Houde and Potthoff 1976).

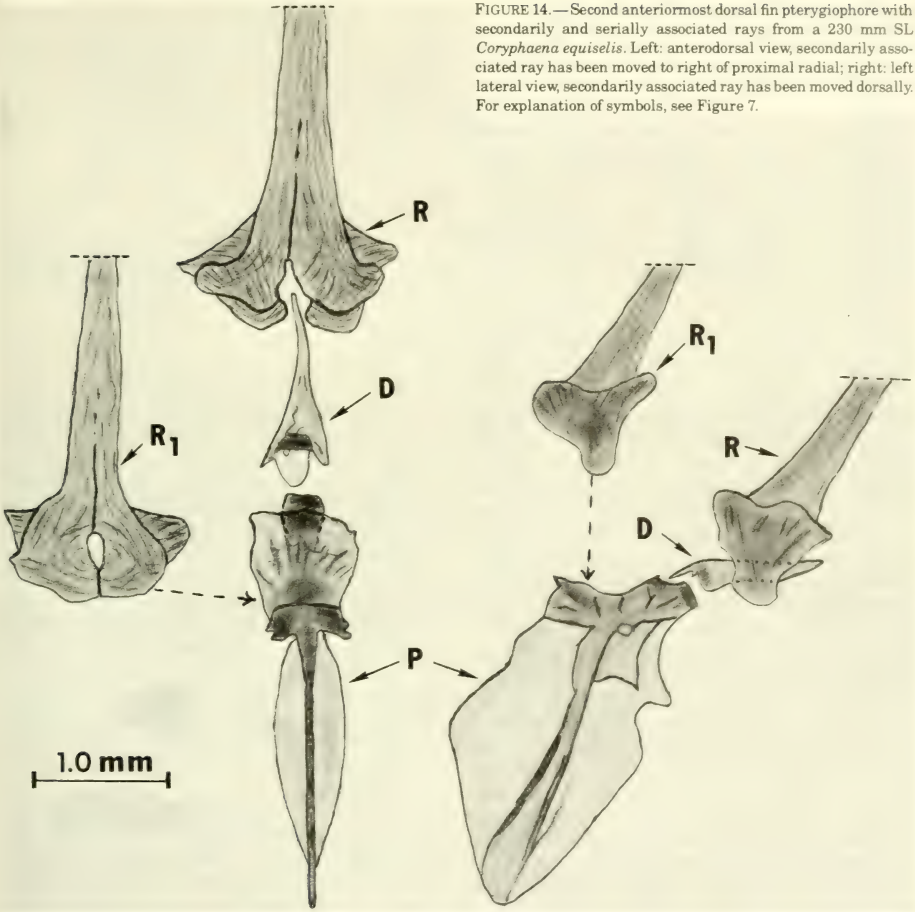


FIGURE 14.—Second anteriormost dorsal fin pterygiophore with secondarily and serially associated rays from a 230 mm SL *Coryphaena equiselis*. Left: anterodorsal view, secondarily associated ray has been moved to right of proximal radial; right: left lateral view, secondarily associated ray has been moved dorsally. For explanation of symbols, see Figure 7.

For *Trachurus symmetricus*, Ahlstrom and Ball (1954) reported an anterior to posterior anal fin development.

Anal Fin Pterygiophores

Counts

The description for dorsal fin pterygiophores in the foregoing section may be applied to anal fin pterygiophores because of the similarities between the two fins and their supports. Pterygiophores of the anal fin are inserted in the interhaemal spaces. The anteriormost (first) interhaemal space is bounded anteriorly by the stomach, intestine, and anus and posteriorly by the first haemal spine. The first haemal spine was of variable length, and in many cases did not reach the anal fin pterygiophores. The anal fin pterygiophores in the two anteriormost interhaemal spaces were therefore summed (Table 5, Figure 3).

Fully developed specimens of *Coryphaena* spp. differed in their numbers and arrangement of anal fin pterygiophores. The total number of pterygiophores closely approximated the anal fin ray count. For both species the pterygiophore count was equal to or one to two less than the anal fin ray count. The sum of the pterygiophores found in the

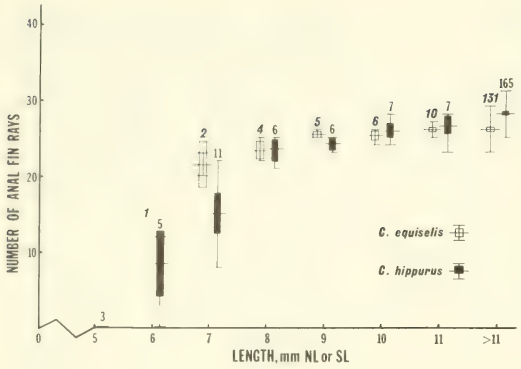


FIGURE 15.—Number of anal fin rays in relation to length in 159 *Coryphaena equiselis* (6.5-230 mm NL or SL) and 210 *C. hippurus* (5.0-230 mm NL or SL). For explanation of symbols, see Figure 1.

first two anteriormost interhaemal spaces (14 and 15) separated the species most of the time, with 7-10 ($\bar{x}$ = 8.0) for *C. hippurus* and 4-7 ($\bar{x}$ = 5.0) for *C. equiselis* (Table 5). The two species also differed in the number of pterygiophores found in the remainder of the interhaemal spaces. Individual variability, however, was too great for each interhaemal space to serve as a separating character. The mean number of pterygiophores for each interhaemal space was always greater for *C. hippurus*. *Coryphaena equiselis* had more interhaemal spaces with one pterygiophore and *C. hippurus* more with two pterygiophores. In *C. hippurus* the anal fin pterygiophores extended to the 25th, 26th, or 27th interhaemal space, but most often to the 26th, whereas in *C. equiselis* they extended to the 27th, 28th, or 29th interhaemal space, but most often to the 28th. There was some overlap for the two species in this character, but if the termination of anal and dorsal fin pterygiophores is considered together, complete separation for the two species results (Table 3). The dorsal and anal fin pterygiophores most often terminated in opposing interneural and interhaemal spaces (Table 3).

Morphology and Development

Cartilaginous anal fin pterygiophores without fin rays were first observed in the 18th-24th myomeres (which approximately correspond to the 18th-24th interhaemal spaces) in a 5.9 mm NL *C. hippurus* (Figure 2, Table 6), but rays were developing in a 6 mm NL specimen. The smallest available *C. equiselis* of 6.5 mm NL had cartilaginous pterygiophores in myomeres 18-27. Fin rays were developing, but a few anteriormost and posteriormost pterygiophores lacked rays. Addition of cartilaginous pterygiophores proceeded in both species anteriorly and posteriorly (Figure 2, Table 6). Rays developed after the addition of the cartilaginous pterygiophores. The posteriormost interhaemal space number 26 of *C. hippurus* had one to three cartilaginous pterygiophores at 7.3-8.3 mm SL (Table 6). The posteriormost interhaemal space number 28 of *C. equiselis* had cartilaginous pterygiophores at 7 mm SL (Table 6). All specimens of *C. hippurus* > 9.5 mm SL and all those of *C. equiselis* > 8.5 mm SL had some pterygiophores in their anteriormost interhaemal space number 14. The size at which adult counts were reached for the first interhaemal space was not determined.

Ossification of the cartilaginous pterygiophores first occurred in the area where the cartilaginous pterygiophores first appeared and proceeded in the same direction as cartilage development (Figure 2). Ossifying anal fin pterygiophores were first seen at 8.8 mm SL in *C. equiselis* and at 9.7 mm SL in *C. hippurus* in the 16th-19th and 16th-25th interhaemal spaces (Table 6), and concurrently with ossifying dorsal fin pterygiophores. The posteriormost interhaemal space number 28 of *C. equiselis* had ossifying pterygiophores at 8.9 mm SL and space number 26 of *C. hippurus* had them at 10.2 mm SL (Table 6). All specimens of *C. equiselis* > 9.4 mm SL and all specimens of *C. hippurus* > 11 mm SL had some ossifying pterygiophores in the anteriormost interhaemal space number 14, or rarely space number 15 (Table 6). The anteriormost anal fin pterygiophore was ossifying in *C. equiselis* at 14.9-22 mm SL and in

TABLE 6.—Development of anal fin pterygiophores in the interhaemal spaces for 46 *Coryphaena hippurus* and 34 *C. equiselis*. For numbering interhaemal spaces, see Figure 3.

Length mm NL or SL	Interhaemal spaces with cartilaginous pterygiophores				Interhaemal spaces with ossifying pterygiophores				Number of specimens	
	Anteriormost space no. (x)		Posteriormost space no. (x)		Anteriormost space no. (x)		Posteriormost space no. (x)			
	C. hippurus	*C. equiselis*	*C. hippurus*	*C. equiselis*	*C. hippurus*	*C. equiselis*	*C. hippurus*	*C. equiselis*	*C. hippurus*	*C. equiselis*
4.6- 5.5	[1]	—	[1]	—	[2]	—	[2]	—	1	—
5.6- 6.5	18-22(19.7)	18	23-24(23.7)	27	[2]	[2]	[2]	[2]	3	1
6.6- 7.5	14-20(17.3)	15	23-26(25.1)	28	[2]	[2]	[2]	[2]	9	1
7.6- 8.5	14-16(14.6)	15-16(15.5)	25-26(25.7)	28	[2]	[2]	[2]	[2]	3	4
8.6- 9.5	14-15(14.4)	14		28	[2]	[2]	[2]	[2]	10	7
9.6-10.5	14	14-15(14.1)	26	28	[3]14-16(15.4)	14-15(14.1)	[3]25-26(25.8)	28	7	9
10.6-11.5	14	14-15(14.1)	26	28	[3]14-18(14.7)	14-15(14.1)	[3]25-26(25.9)	28	9	5
11.6-12.5	14	14	26	28-29(28.2)	14	14	26	28-29	4	

[1]No pterygiophores developed
[2]No pterygiophores ossified

C. hippurus at 17.2-30 mm SL. The development of individual anal fin pterygiophores was similar to that of the dorsal fin pterygiophores.

Each anal fin pterygiophore of both species had two rays; one ray was in a serial association and the preceding ray was in a secondary association. The posteriormost anal ray lacked a secondary association with a pterygiophore and the anteriormost anal ray lacked a serial association (Figure 16). Exceptions were common with the anteriormost pterygiophore and rays. Many specimens of both species had very small first pterygiophores or even vestiges. In a few instances in both species the anteriormost first pterygiophore was completely or partially fused to the second pterygiophore. The normal number of anal rays associated with the first pterygiophore was two, but for both species one or three rays also were found. The anteriormost anal ray was either normal as in Figure 16, very small, or a vestige. As in the dorsal fin, the vestige was either single left or right, or paired.

A distal radial was present between the base of each fin ray almost for the entire anal fin. It developed and ossified from the pterygiophore cartilage. Only the anteriormost anal fin ray sometimes did not have a distal radial between its base (Table 7). Only 1 *C. hippurus* out of 49 had two anteriormost rays without distal radials. When the anteriormost ray had a distal radial, it was either serially or secondarily associated with the first pterygiophore. When the association was serial, the anteriormost pterygiophore had only one ray; when it was secondary, it had two rays. It is possible that, when the association was secondary, the distal radial of the first fin ray was in actuality a vestigial pterygiophore. The specimen in Figure 16 did not have a distal radial for the anteriormost ray. The absence or presence of distal radials for the anteriormost anal fin ray was not related to the number of fin rays that were

TABLE 7.—Number (adult count) of anteriormost anal fin rays without distal radials and number of anal fin rays associated secondarily and serially with the anteriormost anal fin pterygiophore in 49 *Coryphaena hippurus* (41.0-176 mm SL) and 33 *C. equiselis* (74.1-172, 314 mm SL).

Item	Species	Number of anteriormost anal fin rays			
		0	1	2	3
Without distal radials	*C. hippurus*	24	24	1	
	C. equiselis	10	23		
Associated with the anteriormost anal pterygiophore	*C. hippurus*		3	40	6
	C. equiselis		3	29	1

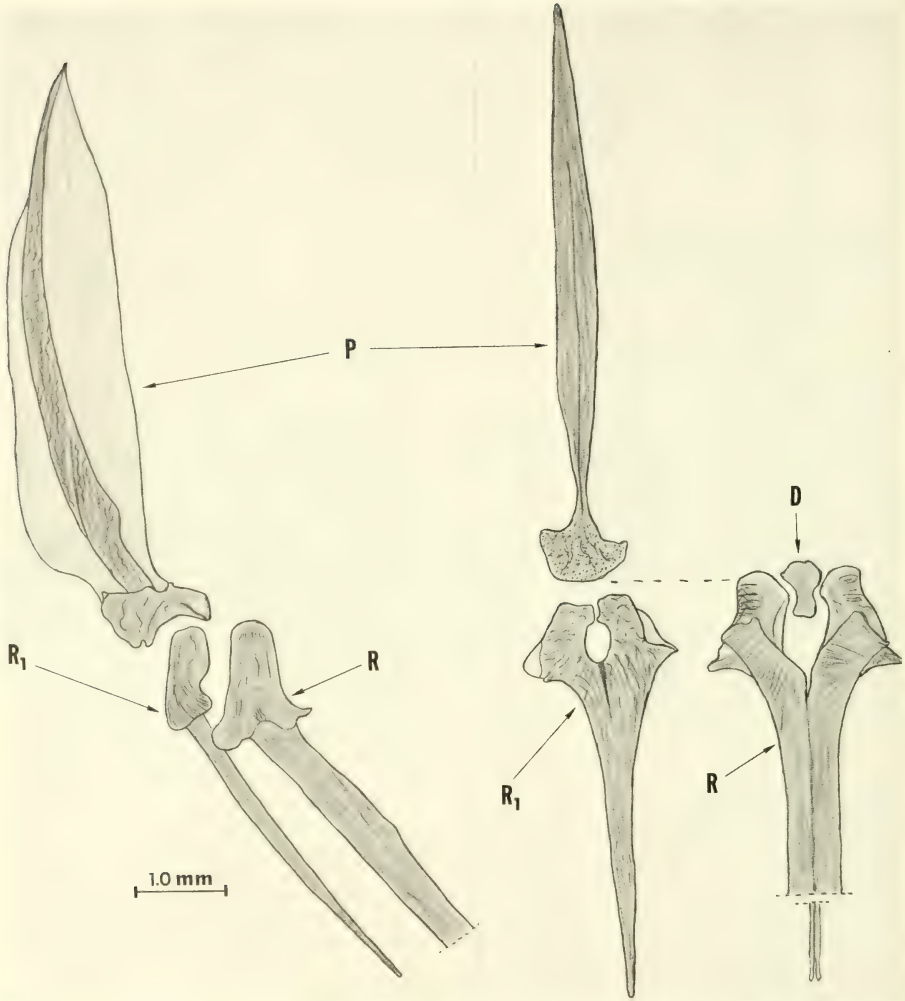


FIGURE 16.—Anteriormost anal fin pterygiophore with secondarily and serially associated rays from a 230 mm SL *Coryphaena equiselis*. Left: left lateral view; right: anterior view, serially associated ray has been moved to the left of the proximal radial. • Symbols: D, distal radial of serially associated ray; P, proximal radial; R_1, secondarily associated ray; R, serially associated ray.

associated with the anteriormost anal pterygiophore (Table 7). In both species either one, two, or three rays were associated with the first pterygiophore. In both species the anteriormost distal radial (which was either between the base of the first or second anal fin ray) was a single piece of bone (Figure 16). The second distal radial (which was either between the base of the second or third anal fin ray) consisted of two pieces of bone, as shown for the dorsal pterygiophores in Figures 7

and 8. The two pieces of the second distal radial were sometimes partially fused; and in a few rare cases, the second distal radial was one piece of bone. All following distal radials of the anal fin were two pieces of bone in both species. The posteriormost anal fin ray consisted of two closely approximated rays with one distal radial.

TABLE 8.—Adult caudal fin ray counts for 117 *Coryphaena hippurus* (19.6-172 mm SL) and 97 *C. equiselis* (19.6-230 mm SL). Symbols: USCR, upper secondary caudal rays; LSCR, lower secondary caudal rays; PCR, principal caudal rays.

Total fin ray count	USCR+PCR+LSCR	Number of specimens	
		C. hippurus	*C. equiselis*
37	10+17+10	0	1
38	10+17+11	2	1
39	10+17+12	0	2
39	11+17+11	10	0
40	11+17+12	12	28
40	12+17+11	3	0
41	11+17+13	0	6
41	12+17+12	36	17
42	12+17+13	23	32
43	13+17+13	26	8
44	13+17+14	2	2
45	14+17+14	3	0

Caudal Fin

The two species differed little in ray counts on fully developed caudal fins. *Coryphaena hippurus* had 38-45 ($\bar{x}$ = 41.4) caudal rays and *C. equiselis* had 37-44 ($\bar{x}$ = 41.1) (Table 8). *Coryphaena hippurus* tended to have an equal number of upper and lower secondary caudal rays whereas *C. equiselis* tended to have one or two more lower than upper secondary caudal rays. Adult caudal ray counts for *C. hippurus* were obtained between 15.6 and 19.6 mm SL and for *C. equiselis* between 11.6 and 12.5 mm SL (Tables 9, 10). A procur-

TABLE 9.—Caudal fin ray development in 201 *Coryphaena hippurus* (5.0 mm NL-172 mm SL) and 138 *C. equiselis* (6.5 mm NL-230 mm SL). Symbols: SCR, secondary caudal rays; PCR, principal caudal rays.

Length mm NL or SL	*Coryphaena hippurus*								*Coryphaena equiselis*							
	Upper		Lower		Total fin ray count				Upper		Lower		Total fin ray count			
	SCR	PCR	PCR	SCR	Range	x	S_x	N	SCR	PCR	PCR	SCR	Range	x	S_x	N
4.6- 5.5	0	2-4	2-5	0	4- 9	7.0	1.5	3	—	—	—	—	—	—	—	—
5.6- 6.5	0	4-8	5-8	0	9-16	11.3	1.6	4	0	6	6	0	12	—	—	1
6.6- 7.5	0	1-8	2-8	0- 1	3-17	12.9	1.3	10	0	9	8	1- 2	18-19	18.5	0.5	2
7.6- 8.5	0	9	8	1- 2	18-19	18.8	0.2	6	0- 3	9	8	2- 4	19-24	21.2	1.2	5
8.6- 9.5	0- 3	9	8	2- 4	19-24	19.8	1.1	5	3- 8	9	8	4- 8	24-33	29.0	1.9	4
9.6-10.5	1- 4	9	8	2- 5	21-26	23.3	0.7	7	5- 9	9	8	6- 9	28-35	31.0	1.3	5
10.6-11.5	0- 4	9	8	2- 5	19-26	24.7	1.0	7	7- 9	9	8	8- 9	32-35	33.6	0.4	7
11.6-12.5	4- 5	9	8	5- 7	26-29	27.7	0.9	3	10-11	9	8	11-12	38-40	38.5	0.5	4
12.6-13.5	5- 6	9	8	6	28-29	28.6	0.2	5	11	9	8	12	40	—	—	1
13.6-14.5	7- 8	9	8	8- 9	32-34	33.3	0.3	6	11	9	8	12	40	—	—	1
14.6-15.5	7- 9	9	8	8-10	32-36	34.7	0.6	6	12	9	8	12	41	—	—	1
15.6-16.5	9-11	9	8	10-12	36-40	37.5	0.7	6	11	9	8	11-13	39-41	40.0	1.0	2
16.6-17.5	9-11	9	8	9-11	35-39	36.6	0.7	5	11	9	8	11-13	39-41	40.0	0.6	3
17.6-18.5	9-11	9	8	9-11	35-39	38.2	0.8	5	11-12	9	8	12-13	40-42	40.5	0.5	4
18.6-19.5	8-12	9	8	12	37-41	39.5	0.6	6	11	9	8	12	40	—	—	1
>19.5	10-14	9	8	11-14	38-45	41.4	0.1	117	10-13	9	8	10-14	37-44	41.1	0.1	97

TABLE 10.—Length (in millimeters NL or SL) at which parts of the caudal complex first appear in cartilage and then ossify in 41 *Coryphaena hippurus* (5.0 mm NL-110 mm SL) and 39 *C. equiselis* (6.5-85 mm SL). "First appearance in cartilage" does not pertain to all specimens of that size but only indicates a first appearance. Symbol: Pu, preural centrum.

Part	*Coryphaena hippurus*				*Coryphaena equiselis*			
	First appearance in cartilage	First evidence of ossification	Ossifying in all specimens	Completely fused	First appearance in cartilage	First evidence of ossification	Ossifying in all specimens	Completely fused
Neural spine, Pu_3	7.4	9.5	11.9	—	>6.5 but <7.6	7.6	8.1	—
Specialized neural arch, Pu_2	7.4	11.9	11.9	—	>6.5 but <7.6	9.5	9.5	—
Large uroneural	—	8.0-10.6	11.9	75.0- 85.0	—	>6.5 but < 7.6	7.6	75.0-80.0
Small uroneural	—	11.9	11.9		—	(9.5?) 10.8	10.8	
Epurals	7.4-8.0	14.6	14.6	40.0- 47.0	>6.5 but <7.6	10.8	10.8	34.0-39.0
Urostyle	—	8.0	11.9	—	—	7.6	7.6	—
Pu_2 centrum	—	9.5	11.9	—	—	7.6	9.5	—
Pu_3 centrum	—	9.5	11.9	—	—	7.6	9.5	—
Haemal spine, Pu_3	6.0	9.5	11.9	—	>6.5	7.6	9.5	—
Haemal spine, Pu_2	5.0	9.5	11.9	—	<6.5	7.6	9.5	—
Parhypural	<5.0	9.5	11.9	—	<6.5	7.6	7.6	—
Hypural 1	<5.0	9.5	11.9	106.0	<6.5	7.6	7.6	69.0
Hypural 2	<5.0	9.5	11.9		<6.5	7.6	7.6	
Hypural 3	<5.0	9.5	11.9	106.0	<6.5	7.6	7.6	69.0
Hypural 4	6.0	9.5	11.9		6.5	7.6	7.6	
Hypural 5	8.1-9.5	11.9	11.9	—	7.6	9.5	9.5	—

rent spur (Johnson 1975) was not observed in either species.

The caudal rays first developed in both species from the midline between hypurals 2 and 3 in preflexion larvae (Figure 17). Rays were added in a posterior and anterior direction (Figure 18). After complete notochord flexure the secondary caudal rays were added in an anterior direction. For equal-sized specimens from 6.5 mm NL to 19.5 mm SL, *C. hippurus* had fewer caudal fin rays than *C. equiselis* (Table 9).

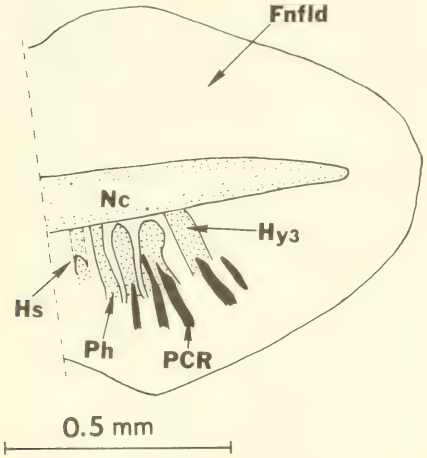


FIGURE 17.—Caudal complex of *Coryphaena hippurus*, 5.0 mm NL. Symbols: Fnfld, finfold; Hs, haemal spine; Hy, hypural; Nc, notochord; PCR, principal caudal ray; Ph, parhypural. Stippled, cartilage; darkened, ossifying bones or rays.

Caudal Fin Supports

The caudal fin rays of *Coryphaena* spp. were supported by some of the bones of the caudal complex. Three posteriormost centra were involved in this support. In 2 out of 97 *C. equiselis* the caudal fin rays were also supported by a fourth centrum. This variation was not observed in *C. hippurus*.

Supporting bones of the caudal complex consisted of three centra (urostyle and preural centra numbers 2 and 3), one neural spine, one specialized neural arch, two autogenous haemal spines, one autogenous parhypural bone, five autogenous hypural bones, two paired uroneural bones, and two epural bones. These parts were seen during development, but not all the parts are readily discerned in the adults due to ontogenetic fusion.

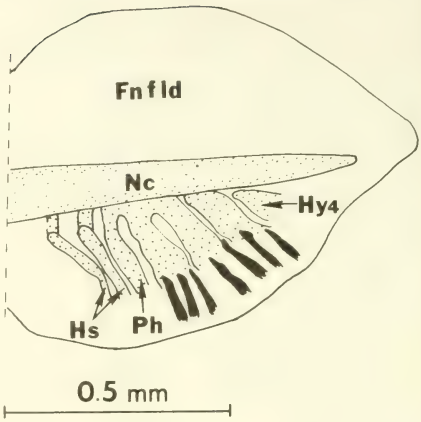


FIGURE 18.—Caudal complex of *Coryphaena hippurus*, 6.0 mm NL. For explanation of symbols, see Figure 17. Stippled, cartilage; darkened, ossifying bones or rays.

The species did not differ in the anatomy of the caudal complex, but they differed in the size at which parts appeared and ossified. The 6.5 mm NL *C. equiselis* was at the same stage of caudal development as a 6.5 mm NL *C. hippurus*. From 7.6 to 16 mm SL, *C. equiselis* was more advanced. Specimens >16 mm SL of both species had the caudal complex equally ossified for the same lengths, but epural, uroneural, and hypural fusions occurred at shorter lengths in *C. equiselis*.

Development of the caudal complex of *C. hippurus* is described here rather than *C. equiselis* because small specimens were not available for *C. equiselis*. Most of the illustrations of the caudal complex are of *C. equiselis* because they were drawn before it was apparent that *C. equiselis* < 7.6 mm were not available. Because both species had identical caudal complex anatomy, no drawings of *C. hippurus*' caudal complex were made for specimens >7.6 mm SL.

At 5 mm NL, *C. hippurus* had a straight notochord. Hypurals 1 to 3, the parhypural, and the haemal spine of the future preural centrum 2 were present in cartilage and 2 + 3 principal caudal rays were counted (Figure 17). At 6 mm NL, hypural 4 and an additional cartilaginous haemal spine of the future preural centrum 3 were present (Figure 18). Notochord flexion in *C. hip-*

purus was between 7 mm NL and 7.5 mm SL, and in *C. equiselis* between 6.5 mm NL and 7.6 mm SL (Figure 19). During the flexion stage of some *C. hippurus* the neural spine of preural centrum 3, the specialized neural arch of preural centrum 2, and the two epurals began to develop from cartilage (Figure 19). Hypural 5 was first seen in cartilage at 8.1 mm SL. The two paired uroneurals did not develop from cartilage—in *C. hippurus* the larger, more ventrally and anteriorly located pair was seen at 8-10.6 mm SL, and the smaller, more dorsally and posteriorly located pair was seen at 11.9 mm SL. Development of the two paired uroneurals occurred at a smaller size in *C. equiselis* (Figure 19 left, Table 10). The smaller uroneural pair gradually fused to the outside of the larger uroneural pair in both species. This fusion was completed between 75 and 85 mm SL for *C. hippurus* and between 75 and 80 mm SL for *C. equiselis* (Table 10). Monod (1968) recognized only one uroneural (stegural) pair in adult *C. hippurus*.

Ossification of the cartilage bones in the caudal complex of *C. hippurus* began with the urostyle at 8 mm SL. Last to ossify at 14.6 mm SL were the two epurals. The ossification sequence of all hypural bones is shown in Table 10. The epurals of *C. hippurus* developed and fused in the same manner as those of *C. equiselis*, although development and fusion were always at a smaller size for *C. equiselis* (Figures 19-23, Table 10). Monod (1968) recognized only one epural for adult *C. hippurus*. In *Coryphaena* spp., hypurals 1 and 2 and hypurals 3 and 4 fused to a dorsal and ventral hypural plate (Figures 20-23, Table 10). During fusion paired bony ventrolateral and dorsolateral articular projections formed on the ventral edge of hypural 3 and on the dorsal edge of hypural 2. These projections became the articulatory surfaces between the dorsal and ventral hypural plates (Figures 20-23). The two hypural plates of *Cory-*

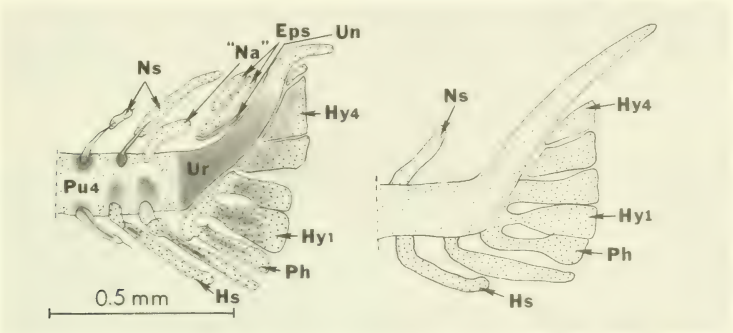


FIGURE 19.—Supporting bones of the caudal complex of *Coryphaena hippurus* (right) 7.6 mm SL and *C. equiselis* (left) 7.6 mm SL. Symbols: Eps, epurals; Hs, haemal spine; Hy, hypural; "Na", specialized neural arch; Ns, neural spine; Ph, parhypural; Pu, preural centrum; Un, uroneural; Ur, urostyle. Stippled, cartilage; darkened, ossifying bones; stippled darkened areas are cartilage just beginning to ossify.

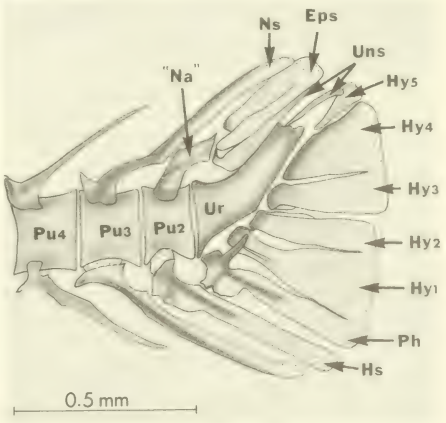


FIGURE 20.—Supporting bones of the caudal complex of *Coryphaena equiselis*, 11.0 mm SL. Symbols: Uns, uroneurals. For explanation of other symbols, see Figure 19. Stippled, articular cartilage; darkened, bone.

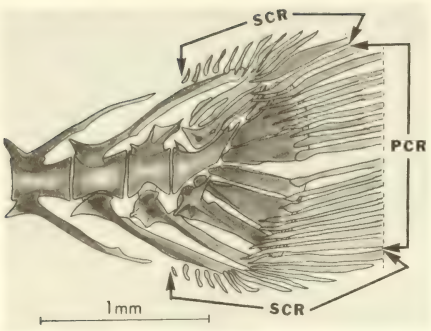


FIGURE 21.—Caudal complex of *Coryphaena equiselis*, 15.9 mm SL. Symbols: PCR, principal caudal rays; SCR, secondary caudal rays. Stippled, articular cartilage; darkened, bone.

autogenous (Figures 23, 24). These were two haemal spines, a parhypural, a ventral and dorsal hypural plate, hypural 5, a uroneural pair (fused from two pairs), and an epural (fused from two). Nonautogenous bones were the specialized neural arch and one neural spine. The relationship of the urostyle with the uroneural pair and hypural 5 is shown in Figure 24. Articular cartilage was present on all distal parts of the hypural complex posterior to preural centrum 4 (Figure 22).

The parhypural and hypurals 1-5 supported the principal caudal rays. The distribution of principal caudal rays on the various hypural bones can only be seen in larvae and smaller juveniles of both species before hypural fusion (Table 11). There was no difference in distribution of principal caudal rays between the two species.

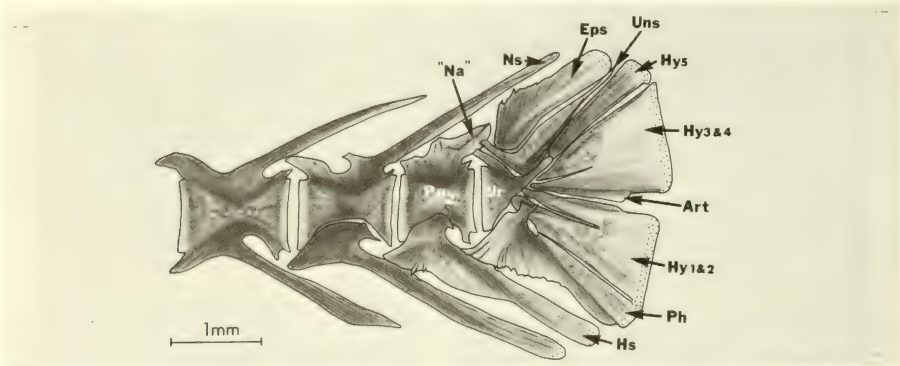


FIGURE 22.—Supporting bones of the caudal complex of *Coryphaena equiselis*, 55.5 mm SL. Symbols: Art, articular projection. For explanation of other symbols, see Figures 19, 20. Stippled, articular cartilage; darkened, bone.

phaena spp. remained autogenous in the adults, but were closely articulated with the ventroposterior edge of the urostyle.

During development of the hypural complex bones a small hypurapophysis (Lundberg and Baskin 1969) was observed on hypural 1 in both species. It appeared before hypural fusion, but could not be illustrated in the lateral view. Disarticulation of adult caudal skeletons of both species of *Coryphaena* revealed the presence of the hypurapophysis. The hypurapophysis articulated with the urostyle just dorsad of the parhypurapophysis (Nursall 1963).

In the adults of *Coryphaena* spp., most bones of the hypural complex were closely articulated, but

The anatomy and development of the caudal complex of *Coryphaena* spp. had similarities and dissimilarities with other fish. The hypurapophysis observed in *Coryphaena* spp. was noted in such fish as siluriform catfish (Lundberg and Baskin 1969) and adult sea bream, *Archosargus rhomboidalis* (Houde and Potthoff 1976). The hypurapophysis was not observed in the blackfin tuna, *Thunnus atlanticus* (Potthoff 1975).

In the Coryphaenidae and other percoid fishes such as Apogonidae (Fraser 1972), *A. rhomboidalis* (Houde and Potthoff 1976), Carangidae (Ahlstrom and Ball 1954; Berry 1969), *Haemulon plumieri* (Saksena and Richards 1975), and some Scombridae (Conrad 1938; Mago Leccia 1958), the

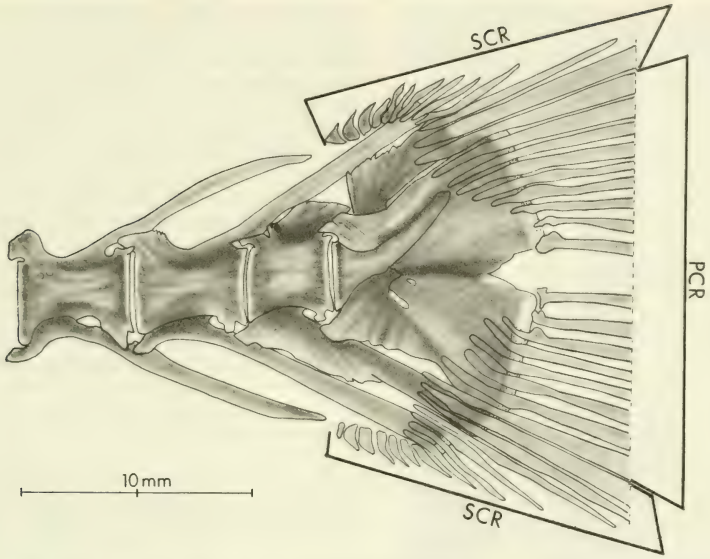


FIGURE 23.—Caudal complex of a *Coryphaena equiselis*, 230 mm SL. For explanation of symbols, see Figure 21. Stippled, articular cartilage; darkened, bone.

TABLE 11.—Distribution of principal caudal rays on the hypurals in 136 *Coryphaena hippurus* (8.0-53 mm SL) (*C. h.*) and 75 *C. equiselis* (7.0-52 mm SL) (*C. e.*).

	Number of principal caudal rays									
	1		2		3		4		5	
Part	*C. h.*	*C. e.*	*C. h.*	*C. e.*	*C. h.*	*C. e.*	*C. h.*	*C. e.*	*C. h.*	*C. e.*
Parhypural			51	24	85	51				
Hypural 1					52	22	80	51	4	2
Hypural 2	39	32	97	43						
Hypural 3			28	27	97	45	11	3		
Hypural 4					6		72	36	58	39
Hypural 5	37	16	98	58	1	1				

epurals were autogenous. In part of the Scombridae (Fierstine and Walters 1968; Monod 1968; Patterson 1968; Collette and Chao 1975; Potthoff 1975) the anteriormost epural is secondarily fused to the specialized neural arch of preural centrum 2. Based on the epurals, *Coryphaena* spp. is advanced because epural numbers are reduced from 3 to 2 and fused to 1 (Patterson 1968; Fraser 1972).

The haemal spines of preural centrum 2 and 3 were autogenous in *Coryphaena* spp. This state is considered basic because advanced percoids have these spines secondarily fused to the centra (Fraser 1972). Fusion of these haemal spines occurs in *T. atlanticus* (Potthoff 1975), and some apogonids (Fraser 1972).

The two prezygapophyses of the urostyle (Figure 24) of *Coryphaena* spp. are true prezygapophyses; whereas in *T. atlanticus* and other Thunnini and Sardini (Collette and Chao 1975; Potthoff 1975) the prezygapophyses of the urostyle represent the pair of uroneurals which have fused to the urostyle during development.

Articular cartilage was present in *Coryphaena* spp. on the caudal complex on all parts distally inclusive of preural centrum 3. No articular cartilage was observed anterior to this centrum. Articular cartilage was observed in scombrids by Fierstine and Walters (1968), in *T. atlanticus* by Potthoff (1975), and in *A. rhomboidalis* by Houde and Potthoff (1975). The absence of articular cartilage in the caudal complex drawings of

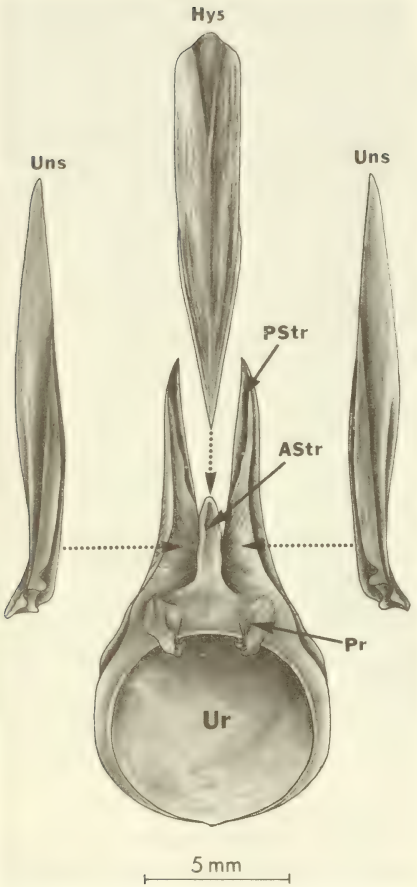


FIGURE 24.—Urostyle of a *Coryphaena equiselis*, 330 mm SL, with disarticulated uroneurals and hypural 5. Dashed lines with arrows point towards place of articulation. Symbols: AStr, anterior strut of urostyle; Hy, hypural; Pr, prezygapophysis; PStr, posterior strut of urostyle; Uns, uroneurals; Ur, urostyle. The articular cartilage is not shown on hypural 5 because of the boiling and drying method of preparation.

apogonids (Fraser 1972) is probably an oversight by the author since he used cleared and stained material. The lack of articular cartilage in most of the drawings of caudal complexes by Monod (1968) can probably be attributed to the method of skeletal preparation, e.g., boiling and subsequent drying.

Autogenous dorsal and ventral hypural plates were observed in adult *Coryphaena* spp. The fusion of individual hypural bones was considered advanced by Fraser (1972). Even more advanced is the fusion of all hypural bones to one hypural plate and the fusion of this plate to the urostyle as in scombrids (Fierstine and Walters 1968; Potthoff 1975).

The formation of articulatory projections of membranous origin during ontogeny at the midline of the caudal complex between the dorsal and ventral hypural plates was observed in *Coryphaena* spp. (Figures 20-22) as well as in *Scombrolabrax heterolepis* (Potthoff et al. 1980), but not in *T. atlanticus* (Potthoff 1975).

Both species of *Coryphaena* had two pairs of uroneurals. The smaller posterior pair gradually moved anteriorly during development and fused to the outsides of the larger anterior pair, until only one pair could be recognized in adults. Fraser (1972) contended that the loss of the posterior pair of uroneurals constituted an evolutionary advance. He did not completely rule out fusion, although he had no evidence for it. There are fishes such as the scombrids which only develop one pair of uroneurals (Potthoff 1975). Loss or fusion of uroneurals can be ascertained through the examination of developmental series.

Pectoral Fin and Supports

The following description is based upon juveniles >13 mm SL of both *Coryphaena* species with adult counts of 19-21 rays. These counts were obtained between 19 and 13 mm SL in *C. equiselis* and between 11 and 13 mm SL in *C. hippurus*. Individual differences in counts between the left and right pectoral fins were lower in both species of *Coryphaena* than in four species of *Thunnus* (Potthoff 1974). Only 1% of 171 *Coryphaena* spp. examined with adult counts >13 mm SL differed by 2 rays between each side, 18% differed by 1 ray, and 81% had the same count on both sides. The pectoral fin rays were directly and indirectly supported on each side by a number of bones which composed the pectoral girdle and its suspensorium. On each side the pectoral girdle consisted of a scapula (which supported the first fin ray directly), four radials (which supported the remainder of the rays directly), a coracoid, and a cleithrum. The scapula and coracoid were connected by cartilage. The suspensorium consisted of seven bones. The supracleithrum and posttemporal were attached

in a row from the outside of the posterior plate of the cleithrum to the rear of the skull and postcleithra 1 and 2 extended over the abdominal area from the inside of the posterior process of the cleithrum. The supratemporal and two intertemporals, which belong with the posttemporal to the laterosensory canal (Harrington 1955), originated just anterior to the posttemporal and ended just short of the supraoccipital crest. Except for individual variation there was no specific difference in the shape of bones of the girdle and suspensorium between the two species. The relationship of bones of the pectoral girdle, suspensorium, and pelvic basipterygium to each other is shown in Figure 25.

Formation of the pectoral fin rays started in the dorsal border of the larval pectoral blade (Figure 26) and continued ventrad (Figure 27). For equal-sized specimens from 6.5 to 13 mm SL, *C. equiselis* had more pectoral fin rays than *C. hippurus* (Figure 28). Of 86 individuals of both species with developing fins <13 mm SL, 5% differed by 2 rays between the left and right sides, 43% differed by 1 ray between the sides, and 52% had the same count on both sides.

The two species differed in length at which development of the pectoral girdle occurred but not in its structure (Table 12). The 6.5 mm NL *C. equiselis* had the same pectoral girdle development as a 6.5 mm NL *C. hippurus*. For individuals of equal length between 7.6 and 18 mm SL, *C. equiselis* was more advanced. At lengths >18 mm SL specimens of both species had the pectoral girdle equally developed except for the supratemporal-intertemporal bones which were first seen at 13 mm SL in *C. equiselis* and at 18 mm SL in *C. hippurus*.

Regarding development of the pectoral girdle in *C. hippurus*, the smallest (5 mm NL) specimen had a simple rod-shaped, bony cleithrum, and a coraco-scapular cartilage (Figure 26). The car-

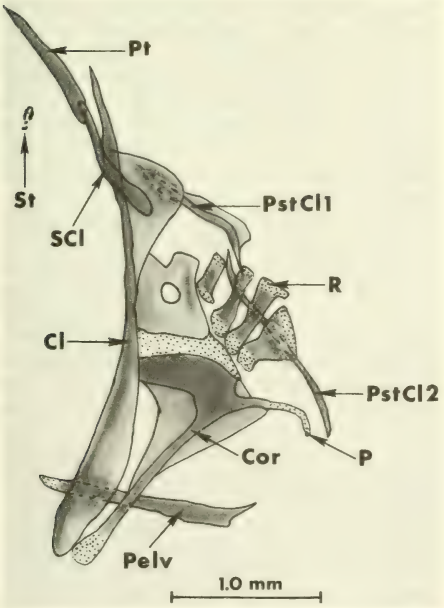


FIGURE 25.—Lateral external view of left sides of pectoral girdle and suspensorium from a 20.8 mm SL *Coryphaena hippurus*. Symbols: Cl, cleithrum; Cor, coracoid; P, posterior process of the coraco-scapular cartilage; Pelv, pelvic basipterygium; PstCl 1, postcleithrum 1; PstCl 2, postcleithrum 2; Pt, posttemporal; R, radial; SCl, supracleithrum; St, supratemporal (beginning to develop). Stippled, cartilage; darkened, bone.

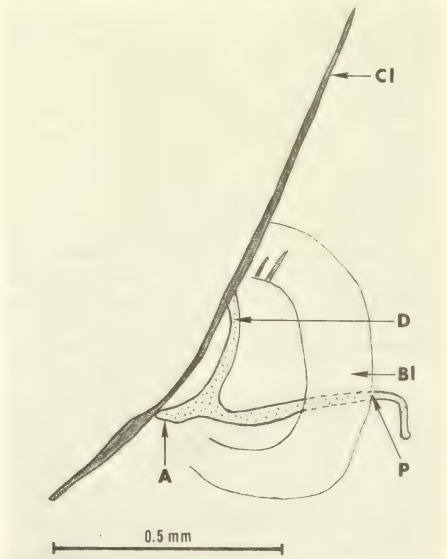


FIGURE 26.—Lateral external view of left side of pectoral girdle from a 5.0 mm NL *Coryphaena hippurus*. Symbols: A, anterior process of the coraco-scapular cartilage; Bl, blade of the larval pectoral fin with two fin rays developing dorsally; Cl, cleithrum; D, dorsal process of the coraco-scapular cartilage; P, posterior process of the coraco-scapular cartilage. Stippled, cartilage; darkened, bone.

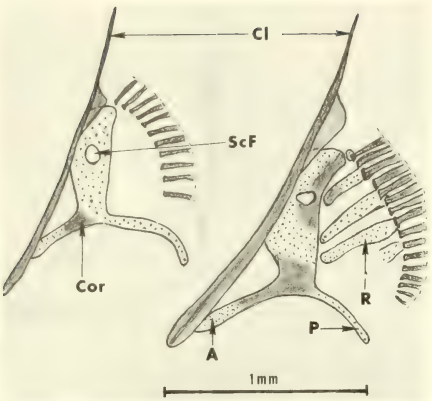


FIGURE 27.—Lateral external view of left side of pectoral girdle from a 8.1 mm SL *Coryphaena hippurus* (left) and a 7.9 mm SL *C. equiselis* (right). Symbols: ScF, scapular foramen. For explanation of other symbols, see Figures 25, 26. Stippled, cartilage; darkened, bone.

tilage consisted of a long dorsal process, a long posterior process, and a short anterior process. Houde and Potthoff (1976) found that the anterior process of the coraco-scapular cartilage formed after the formation of the dorsal and posterior processes in laboratory-reared *Archosargus rhomboidalis* larvae. I believe that both species of *Coryphaena* have the same kind of cartilage development as *A. rhomboidalis*. At 5.5 mm NL, *C. hippurus* first developed the supracleithrum, and after 6.3 mm NL, it was always present. The supracleithrum at first was a small rod-shaped bone, which only gradually acquired its flattened paddlelike shape. The cleithrum and the coraco-scapular cartilage did not show any development between 5 and 7.3 mm NL. The posttemporal first developed as a small, rod-shaped bone at 6.3 mm NL. In larvae of 7.4 mm SL the scapular foramen was first seen in the dorsal process of the coraco-scapular cartilage, and at 7.6 mm SL the posterior process of the cleithrum first appeared (Figure 27). Between 7.6 and 8.4 mm SL many developmental changes occurred. In an 8 mm SL specimen the first dorsalmost radial was seen in cartilage; the radial was absent in an 8.1 mm SL specimen (Figure 27), but present again at 8.3 mm SL. The bony rod-shaped postcleithrum 2 was first seen at 8.3 mm SL. Ossification of the coraco-scapular cartilage started at 8.1 mm SL in the region of the future coracoid at the juncture of the dorsal and anterior processes. The scapula started to ossify first around the scapular foramen at 9.5 mm SL. Also at 9.5 mm SL the postcleithrum 1 was first seen as a tiny speck of bone, but not until 11.9 mm SL was this structure easy to see. All four radials were present at 11.9 mm SL; the dorsalmost was starting to ossify and the following three were in cartilage. All radials in *C. hippurus* were ossifying by 12.3 mm SL (Figure 29). The supratemporal was first seen at 18 mm SL as a single lateral line pore situated anterior to the posttemporal (Figure 25). Its development was difficult to trace because the adult bone was very thin, but distinctive because it was traversed by a lateral line canal. With increasing size more pores appeared, some at a distance dorsad for the two intertemporals and others adjacent to the first pore for the supratemporal. These pores eventually joined to form two tubular canal bones, the intertemporals and the thin supratemporal. Further development of the bones in the pectoral girdle and suspensorium of *C. hippurus* past 12.3 mm SL (when all component bones are ossi-

TABLE 12.—Development of structures, bones and fin rays of the pelvic and pectoral girdles for the two species of *Coryphaena*, shown for lengths (in millimeters NL or SL) at which structures, bones or fin rays first appear in cartilage or ossify. Lengths given signify a first observance and do not necessarily apply to all specimens of that length or longer.

Part	First appearance in cartilage		First evidence of ossification (Stain uptake)	
	C. hippurus	*C. equiselis*	*C. hippurus*	*C. equiselis*
Cleithrum	—	—	not known	not known
Scapula	not known	not known	9.5	7.0
Scapular foramen	7.4	7.0	—	—
Coracoid	not known	not known	8.1	7.0
Radials 1-4	8.0-11.9	8.0-8.9	11.9-12.3	8.8- 9.8
Posttemporal	—	—	6.3	not known
Supracleithrum	—	—	5.5	not known
Postcleithrum 1	—	—	9.5	8.9
Postcleithrum 2	—	—	8.3	7.4
Supratemporal-intertemporals	—	—	18.0	13.0
Pectoral fin rays	—	—	5.0	not known
Pelvic basipterygium	7.0	(6.0?) 7.0	8.7	8.7
Pelvic fin rays	—	—	7.0	7.3

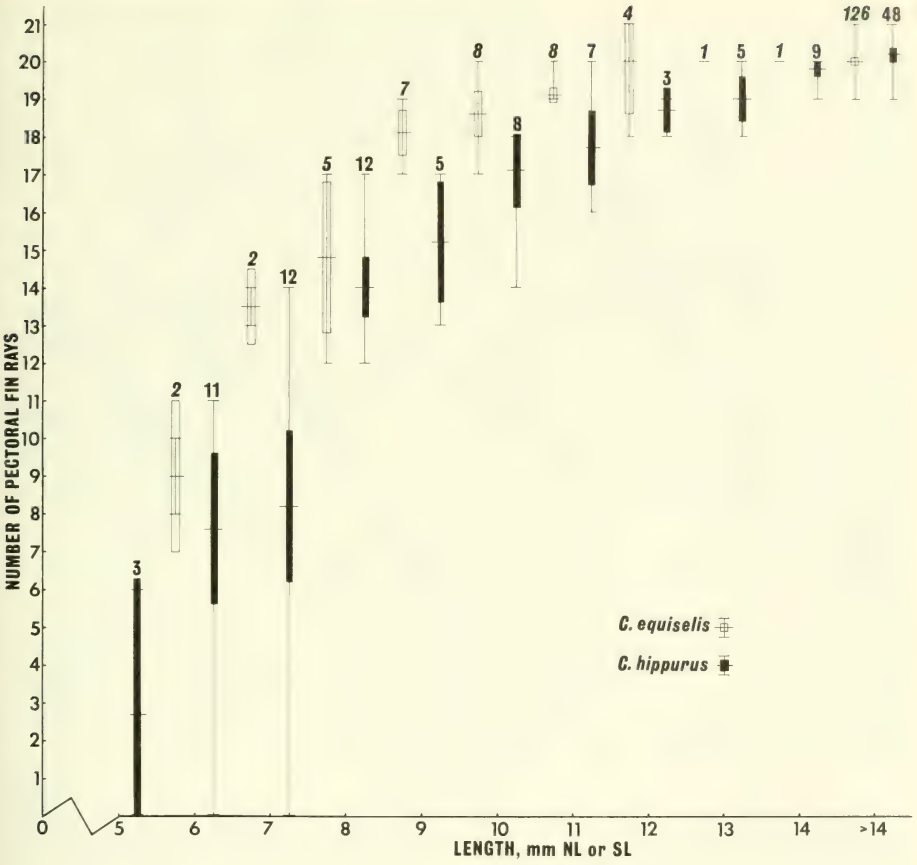


FIGURE 28.—Number of left pectoral fin rays in relation to length in 164 *Coryphaena equiselis* (6.5-230 mm NL or SL) and 123 *C. hippurus* (5-172 mm NL or SL). For explanation of symbols, see Figure 1.

fying, except the supratemporal-intertemporals) consisted of ossification and growth of the bones, and the formation of bony shelves on the cleithrum, coracoid, posttemporal, and postcleithrum 1 (Figures 29, 30). The supratemporal developed thin membranous bones around the lateral line canal tubes. Development also involved loss of cartilage. The cartilage separating the scapula and coracoid became narrower with increasing length (Figures 29, 30). The cartilage from the prominent larval posterior process of the coracoid completely disappeared by 40 mm SL (Figure 30).

No developmental studies of the pectoral fin and supports have been done for *Coryphaena* spp. Starks (1930) studied the anatomy of the pectoral girdle in a variety of adult bony fishes including *C. hippurus*. The development of the coraco-scapular cartilage to a scapula and a coracoid bone and some or total atrophy of the cartilaginous posterior process of the coracoid occurs in most fishes (Swinnerton 1905; Starks 1930). More recently Houde and Potthoff (1976) observed the atrophy of the posterior process in *A. rhomboidalis* and Saksena and Richards (1975) reported the presence

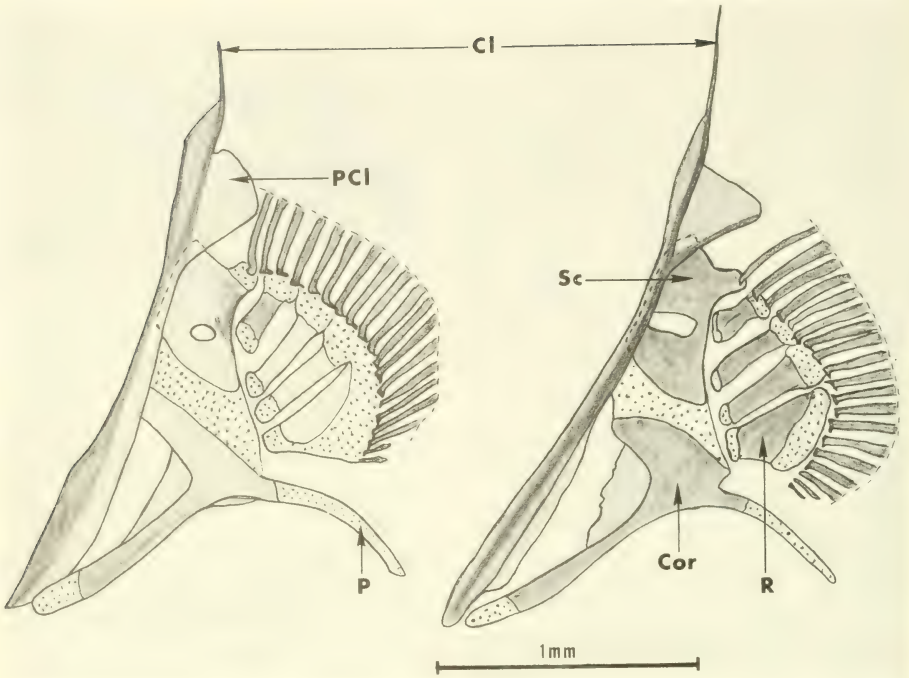


FIGURE 29.—Lateral external view of left side of pectoral girdle from a 12.3 mm SL *Coryphaena hippurus* (left) and a 10.3 mm SL *C. equiselis* (right). Symbols: Cl, cleithrum; Cor, coracoid; P, posterior process of the coraco-scapular cartilage; PCl, posterior process of the cleithrum; R, radial; Sc, scapula. Stippled, cartilage; darkened, bone.

of a Y-shaped cartilaginous coracoid (probably coraco-scapular cartilage) in *Haemulon plumieri* larvae. In the Blenniidae, Characidae, and Pholidichthyidae, a small posterior process of the coracoid was observed in adults (Weitzman 1962; Springer 1968; Springer and Freihofer 1976). For the family Gobiesocidae, however, Springer and Fraser (1976) reported large posterior processes of the coracoid. Thus, it seems that the posterior process of the coracoid is present in most fishes, but that it disappears during development in more advanced forms. It also appears that this process remains as a neotenic structure in small fishes.

In more primitive fishes such as the Osteoglossidae (Greenwood and Thomson 1960), Characidae (Weitzman 1962), most stomiatoid families (Weitzman 1974), and *Lile piquitinga* (Clupeidae) (Gomez Gaspar 1976) a mesocoracoid was present. This bone is absent in the Coryphaenidae.

The presence of intertemporals is considered primitive because these bones are absent in more advanced groups, such as scombrids (Collette and Chao 1975).

Pelvic Fin and Fin Supports

Description is based on large juveniles of both species >90 mm SL, two adults of *C. equiselis* and two adults of *C. hippurus*. There were I,5 rays in each of the pelvic fins which were located on the underside of the body below the pectoral fin. All *C. hippurus* >10.7 mm SL and all *C. equiselis* >8.6 mm SL had the full count. Each side of the pelvic fin was supported by a basipterygium; no radials were present. The two basipterygia were closely approximated medially, but not fused (Figure 31). They were located in the abdominal body wall and were lying between the ventral portions

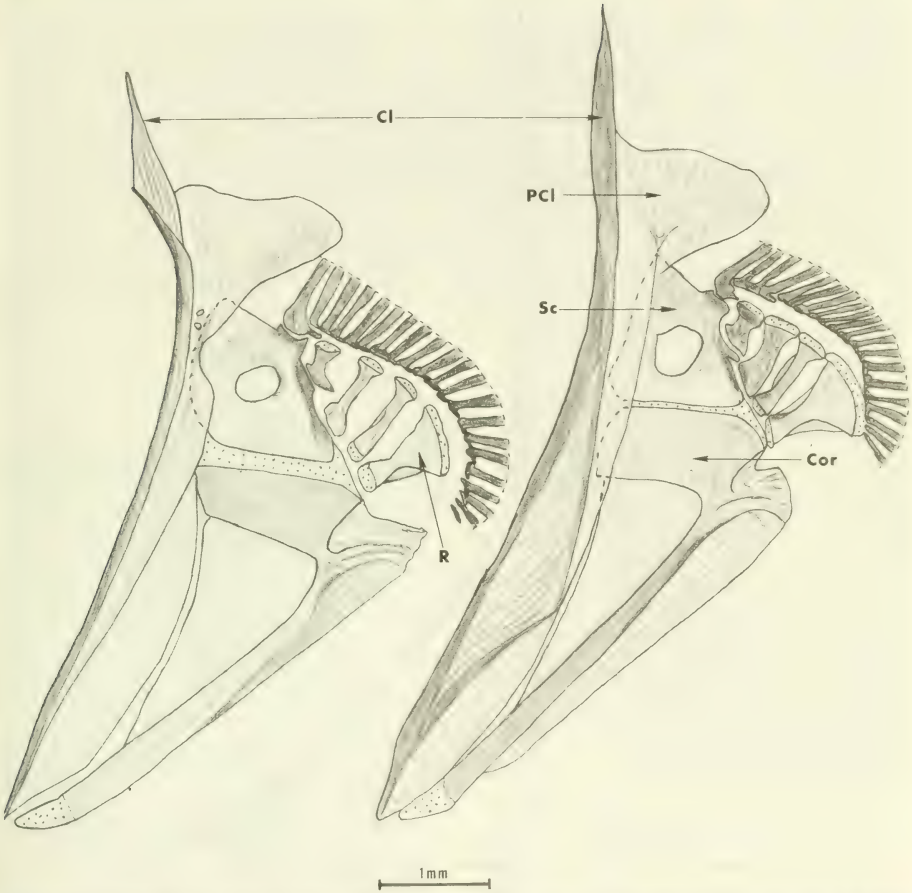


FIGURE 30.—Lateral external view of left side of pectoral girdle from a 47.6 mm SL *Coryphaena hippurus* (left) and a 48 mm SL *C. equiselis* (right). For explanation of symbols, see Figure 29. Stippled, cartilage; darkened, bone.

of the two cleithra and coracoids (Figure 25). No fleshy interpelvic processes were present between the bases of the fins.

The basipterygium is a complex bone. For convenience of description, it was divided into three parts which corresponded to the ontogeny of the bone: the central part, which was the original cartilage, the wings (Kishinouye 1923) of membranous bone origin, and the two xiphoid processes (de Sylva 1955), of which the posterior process was of cartilage origin and the anterior process of bone origin. The central part of the basipterygium carried the four wings along its length (Figures 31-33). Anteriorly the central part was tipped by a small piece of cartilage. Posteriorly the central part served the articulation of the fin rays. A thin layer of articular cartilage was present in adults on the posteriormost portion of the central part (Figures 31, 32). Each basipterygium had four wings, reminiscent of the two sagittal and two lateral keels of pterygiophores. The wings formed a dorsal and a ventral "V" shaped groove, and a

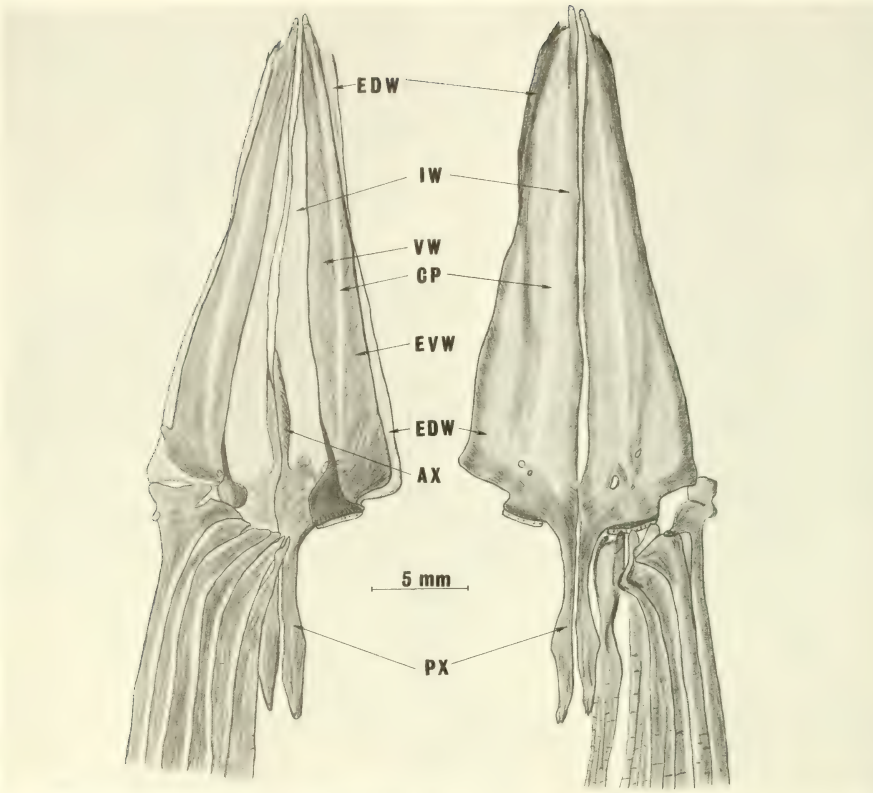


FIGURE 31.—Pelvic fin and basipterygia from a 449 mm SL *Coryphaena hippurus*. Left: ventral external view; right: dorsal internal view. Left pelvic fin has been removed. Symbols: AX, anterior xiphoid process; CP, central part; EDW, external dorsolateral wing; EVW, external ventrolateral wing; IW, internal dorsolateral wing; PX, posterior xiphoid process; VW, ventral wing. Stippled, cartilage; darkened, bone.

lateral "[" shaped channel (Figure 33). The xiphoid processes were located internally at the midline on the basipterygia (Figures 31-33). The anterior xiphoid process was an anteroventral extension of the posterior xiphoid process (Figure 32). The posterior xiphoid process, which pointed in a posterodorsal direction was attached to the posterior part of the basipterygium by a heavy bony strut from the central part and anteriorly by the internal dorsolateral wing (Figures 32, 33). The two basipterygia were closely approximated at the edges of the two internal dorsolateral wings and the internal surfaces of the four xiphoid processes (Figure 31). The closest approximation was observed on the xiphoid processes at the place where the anterior and posterior processes were joined (Figure 32). Here the bone was rough with minute projections. These projections gave a close fit when the surfaces were brought together and prevented the basipterygia from sliding.

No anatomical differences in the development of the pelvic fin and supports were found between *C. hippurus* and *C. equiselis*. Larval and juvenile specimens of *C. equiselis* were more advanced in pelvic development than equal-sized specimens of *C. hippurus* (Table 13; Figures 34, 35). In both

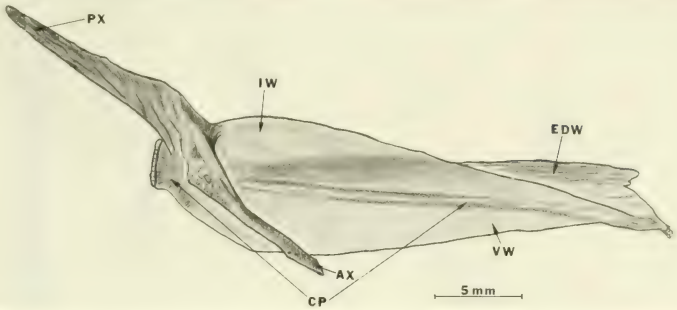


FIGURE 32.—Lateral internal view of left basipterygium from a 449 mm SL *Coryphaena hippurus*. For explanation of symbols, see Figure 31. Stippled, cartilage; darkened, bone.

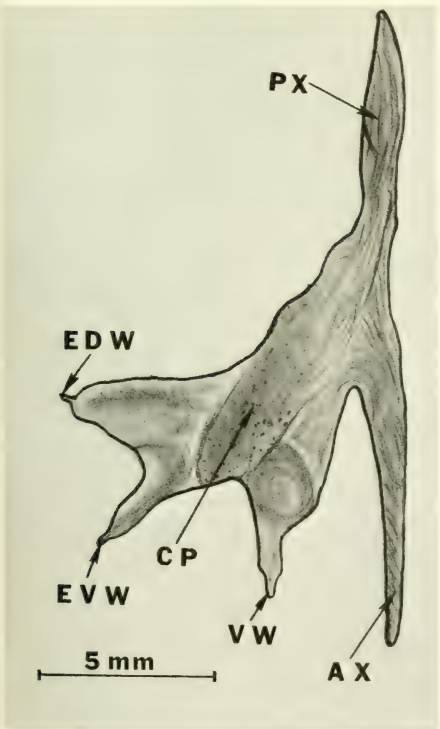


FIGURE 33.—Posterior view of left basipterygium after left pelvic fin had been removed from a 449 mm SL *Coryphaena hippurus*. For explanation of symbols, see Figure 31.

species a fin bud developed first on the abdomen (Table 13). Simultaneously to the fin bud appearance, two cartilaginous basipterygia developed internally at 7 mm SL in flexion larvae of *C. hippurus*. In *C. equiselis* it probably occurred in flexion larvae between 6 and 7 mm SL, but the smallest available specimen measured 7 mm SL (Table 12). The pelvic fin rays developed in the fin bud after basipterygium formation. Fin ray appearance was from the outside of the specimen towards its midline in both species, so that the first ray to appear was the spinous ray. In *C. hippurus* the pelvic fin ray development began at 7-7.5 mm SL and was completed at 10.7 mm SL, and in *C. equiselis* it began at 7.3 mm SL and was completed at 8.6 mm SL.

Each cartilaginous basipterygium in both species was cylindrical with its base expanded posteriorly near the fin bud (Figure 34). The cartilaginous projection of the posterior xiphoid process developed posteriorly at the inner corner of the expanded base (Figure 34). Ossification of the basipterygium cartilage to the central part began in both species at the center and progressed anteriorly and posteriorly as the larvae grew (Figure 34). For *C. hippurus* it began at 8.7-10.8 mm SL, and for *C. equiselis* at 8.7 mm SL (Tables 12, 13). After the cartilaginous central part of the basipterygium had ossified, all structures of membranous origin developed simultaneously; these were the anterior xiphoid process and the four wings (Figure 34). All wings developed from the base in an anterior direction. The posterior xiphoid process was of cartilage origin and started

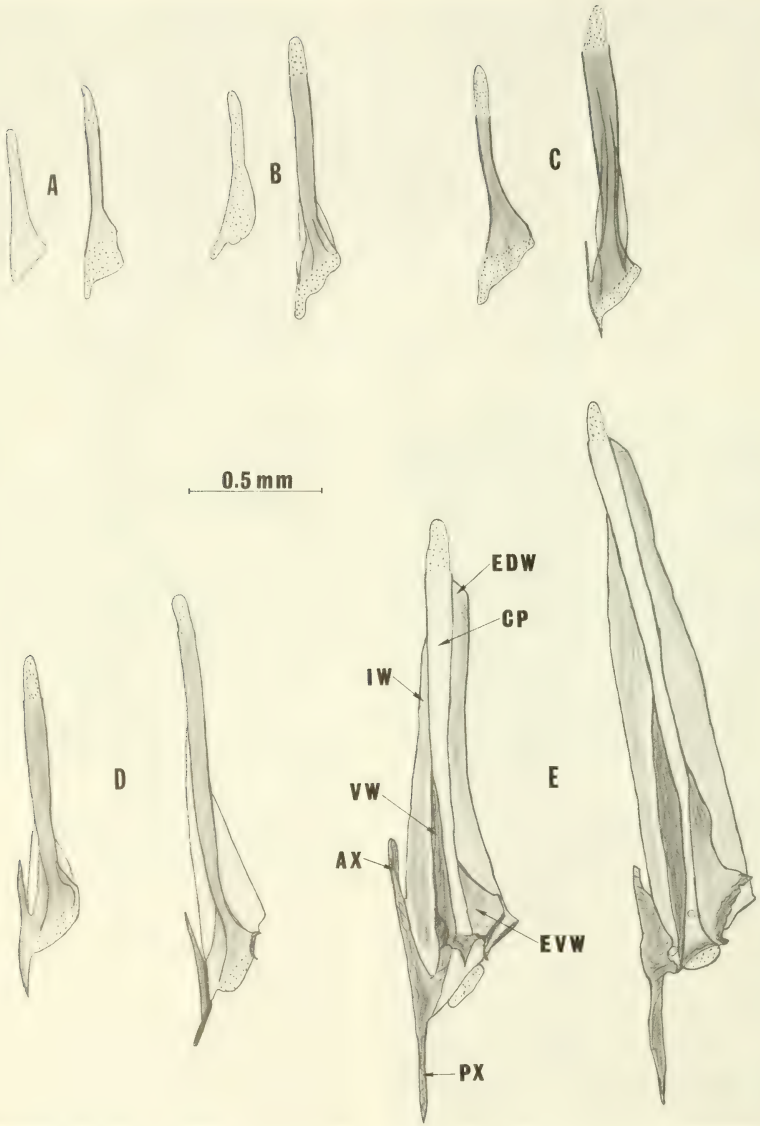


FIGURE 34.—Development of left basipterygium of *Coryphaena* spp. Basipterygium of *C. hippurus* is to left of letters, that of *C. equiselis* is to right. Lengths: A, 8.3 and 8.9 mm SL; B, 10.3 and 10.1 mm SL; C, both 11.3 mm SL; D, 14.1 and 14.2 mm SL; E, 21 and 20.9 mm SL. For explanation of symbols, see Figure 31. Stippled, cartilage; darkened, bone.

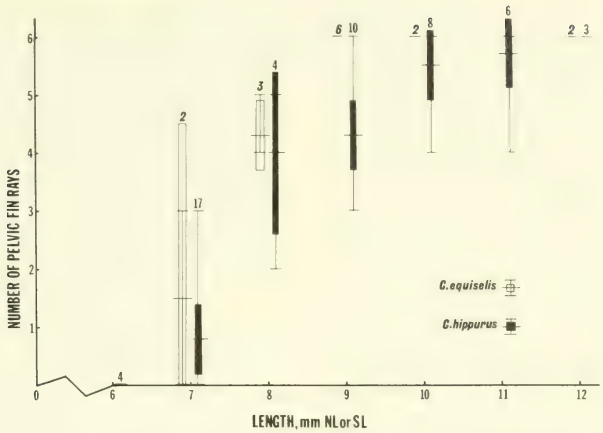


FIGURE 35.—Number of pelvic fin rays in relation to length in 15 *Coryphaena equiselis* (7.0-12.4 mm SL) and 52 *C. hippurus* (6.0-12.5 mm NL or SL). For explanation of symbols, see Figure 1.

TABLE 13.—Development of pelvic fin and supports in 52 *Coryphaena hippurus* (6.0 mm NL-12.5 mm SL) (*C. h.*) and 15 *C. equiselis* (7.0-12.4 mm SL) (*C. e.*). Numbers denote number of specimens, dashes denote specimens not available.

Length mm NL or SL	Fin bud				Fin rays				Basipterygia					
	Absent		Present		Absent		Present		Absent		Cartilaginous		Ossifying	
	C. h.	*C. e.*	*C. h.*	*C. e.*	*C. h.*	*C. e.*	*C. h.*	*C. e.*	*C. h.*	*C. e.*	*C. h.*	*C. e.*	*C. h.*	*C. e.*
5.6- 6.5	4	—	0	—	4	—	0	—	4	—	0	—	0	—
6.6- 7.5	6	0	11	2	12	1	5	1	10	0	7	2	0	0
7.6- 8.5	0	0	4	3	0	0	4	3	0	0	4	3	0	0
8.6- 9.5	0	0	10	6	0	0	10	6	0	0	9	0	1	6
9.6-10.5	0	0	8	2	0	0	8	2	0	0	1	0	7	2
10.6-11.5	0	—	6	—	0	—	6	—	0	—	1	—	5	—
11.6-12.5	0	0	3	2	0	0	3	2	0	0	0	0	3	2

to ossify shortly after the appearance of the anterior xiphoid process (Figure 34).

A comparison of pelvic bones of *Coryphaena* spp. with those of more primitive fishes revealed the absence of radials in *Coryphaena* spp. It is not known if the radials have been lost, or if they have fused to the central part and the articular cartilage during evolution. In the more primitive stomiatoid fish families (Weitzman 1974) and in *Lile piquitinga* (Gomez Gaspar 1976), radials are present between the bases of the fin rays.

DISCUSSION

In a tentative classification of the Perciformes, Greenwood et al. (1966) placed the Coryphaenidae to follow the family Carangidae. This placement was arbitrary because *Coryphaena* spp. is more advanced than some families that follow in the placement.

The one continuous dorsal fin of *Coryphaena* spp. extends to the head, so that the first interneural space, bounded by the head bones and the first neural spine, is occupied by pterygiophores which support the fin rays. Smith and Bailey (1961) contended that the dorsal fin of *Coryphaena* spp. represents an evolutionary advance and specialization because of its anterior extension and the loss or reoccupation by fin rays of the predorsal bones. In diverse fishes, such as characins, sparids, carangids, scombrids, and lutjanids, the pterygiophores in the posterior parts of the dorsal and anal fins have three parts. This triserial pterygiophore structure is considered basic (Eaton 1945; Lindsey 1955; Johnson 1978). Most pterygiophores in *Coryphaena* spp. are biserial, and one or two anteriormost ones uniserial. Thus, the pterygiophores of

Coryphaena spp. are more advanced or specialized due to either a loss or fusion of the middle radial. The loss of the "stay" for the posteriormost dorsal and anal pterygiophore also represents an advance. Therefore, based on the dorsal and anal fin and supports, placement of *Coryphaena* spp. should be phylogenetically higher than that given by Greenwood et al. (1966).

The vertebral number is higher for *C. equiselis* than for *C. hippurus* (Jordan and Evermann 1896; Collette et al. 1969), yet *C. equiselis* has fewer dorsal fin rays than *C. hippurus*. *Coryphaena equiselis* also tends to have fewer anal fin rays than *C. hippurus*. Therefore, since fin ray number is approximately equal to the pterygiophore number, *C. equiselis* has fewer dorsal pterygiophores arranged in more interneural spaces, and *C. hippurus* has more dorsal pterygiophores arranged in fewer interneural spaces. The situation is similar for the anal fin. It is noteworthy that the same number of vertebrae is found in both species posteriorly to the end of the dorsal and anal fins (Figure 3). The evolutionary significance of the relationship between vertebral numbers and pterygiophore numbers is not understood (Lindsey 1955), but may be phylogenetically important.

During development, except for the presence of two rather than three epurals, *Coryphaena* spp. have the basic (unreduced) perciform caudal skeleton (Gosline 1961a; Monod 1968; Patterson 1968; Fraser 1972). Adults of *Coryphaena* spp., however, have a more advanced caudal skeleton. The presence of a single epural and uroneural, as well as a dorsal and ventral hypural plate, shows advance over the basic type, although the fused parts remain autogenous. In the modified and advanced caudal complex of most Scombridae these parts may be fused to the centra. For example, the epural may be fused to the specialized neural arch, the uroneurals and hypural plates may be fused to the urostyle, the parhypural and the hypural plate may be fused to the urostyle, and two haemal spines may be fused to preural centra 2 and 3.

The pectoral skeletons of *Coryphaena* spp. are of the basic perciform type. The pectoral supports fit the description of Greenwood et al. (1966) for the Acanthopterygii. The presence of supratemporal-intertemporal bones and two postcleithra in *Coryphaena* spp. characterize them as a basic perciform pectoral support system. Some fishes may lose some or all supratemporal-intertemporal bones (Scombridae) and some also may lose a postcleithrum (*Gymnapogon*, Apogonidae, Fraser 1972; *Xiphias gladius*, author's personal observation).

The pelvic fin and supports are of the acanthopterygian (perciform) type, one bone supporting an unbranched and five branched rays in a thoracic position. The development and structure of the pelvic basipterygium is similar to that of a pterygiophore. The central part and wings of the basipterygium closely resemble proximal radials with sagittal and lateral keels.

ACKNOWLEDGMENTS

I wish to thank William J. Richards, Francis Williams, and Gilbert L. Voss for critical comments on the manuscript. Special thanks are due to Edward D. Houde for help with statistics and for a most thorough review of the manuscript. I thank Elbert H. Ahlstrom for reading the manuscript and for his comments, especially for those on the caudal complex.

I thank the persons that supplied me with specimens: Elbert H. Ahlstrom, Bruce B. Collette, Edward D. Houde, William J. Richards, C. Richard Robins, Frederick H. Berry, and George C. Miller.

For typing numerous drafts of the manuscript, I am grateful to Phyllis Fisher, and for proofreading numerous drafts I thank Teresa Ratajczak and Kelly Clark. I also thank Grady Reinert, Annalee Green, and Joaquin Javech for inking the caudal complex drawings and for labeling all the drawings in the manuscript; Andrew J. Ramsay, Jr. for the photographic work; Mal M. Brassfield and Scott Quaas with the clearing and staining of the study specimens; and Bruce B. Collette and Frank J. Mather III for providing some original data on *Coryphaena* spp.

LITERATURE CITED

AHLSTROM, E. H., AND O. P. BALL.
1954. Description of eggs and larvae of jack mackerel (*Trachurus symmetricus*) and distribution and abundance of larvae in 1950 and 1951. U.S. Fish Wildl. Serv., Fish. Bull. 56:209-245.

AHLSTROM, E. H., J. L. BUTLER, AND B. Y. SUMIDA.
1976. Pelagic stromateoid fishes (Pisces, Perciformes) of the eastern Pacific: kinds, distributions, and early life histories and observations on five of these from the northwest Atlantic. Bull. Mar. Sci. 26:285-402.

BEARDSLEY, G. L., JR.
1967. Age, growth, and reproduction of the dolphin, *Coryphaena hippurus*, in the Straits of Florida. Copeia 1967: 441-451.

BERRY, F. H.
1969. *Elagatis bipinnulata* (Pisces: Carangidae): morphology of the fins and other characters. Copeia 1969: 454-463.
BURNETT-HERKES, J.
1974. Parasites of the gills and buccal cavity of the dolphin, *Coryphaena hippurus*, from the Straits of Florida. Trans. Am. Fish. Soc. 103:101-106.
CLOTHIER, C. R.
1950. A key to some Southern California fishes based on vertebral characters. Calif. Dep. Fish Game, Fish. Bull. 79, 83 p.
COLLETTE, B. B., AND L. N. CHAO.
1975. Systematics and morphology of the bonitos (*Sarda*) and their relatives (Scombridae, Sardini). Fish. Bull., U.S. 73:516-625.
COLLETTE, B. B., R. H. GIBBS, JR., AND G. E. CLIPPER.
1969. Vertebral numbers and identification of the two species of dolphin (*Coryphaena*). Copeia 1969:630-631.
CONRAD, G. M.
1938. The osteology and relationships of the wahoo (*Acanthocybium solandri*), a scombroid fish. Am. Mus. Novit. 1000, 32 p.
DE SYLVA, D. P.
1955. The osteology and phylogentic relationships of the blackfin tuna, *Thunnus atlanticus* (Lesson). Bull. Mar. Sci. Gulf Caribb. 5:1-41.
EATON, T. H., JR.
1945. Skeletal supports of the median fins of fishes. J. Morphol. 76:193-212.
FIERSTINE, H. L., AND V. WALTERS.
1968. Studies in locomotion and anatomy of scombroid fishes. Mem. South. Calif. Acad. Sci. 6:1-31.
FRASER, T. H.
1972. Comparative osteology of the shallow water cardinal fishes (Perciformes: Apogonidae) with reference to the systematics and evolution of the family. Rhodes Univ., Dep. Ichthyol., Ichthyol. Bull. 34:1-105.
GIBBS, R. H., JR., AND B. B. COLLETTE.
1959. On the identification, distribution, and biology of the dolphins, *Coryphaena hippurus* and *C. equiselis*. Bull. Mar. Sci. Gulf Caribb. 9:117-152.
GOMEZ GASPAR, A.
1976. Osteologia de *Lile piquitinga* (Schreiner y Miranda Ribeiro 1903) (Pisces Clupeidae). Bol. Mus. Mar. Bogotá 8:1-52.
GOSLINE, W. A.
1961a. The perciform caudal skeleton. Copeia 1961: 265-270.
1961b. Some osteological features of modern lower teleostean fishes. Smithson. Misc. Collect. 142(3):1-42.
GREENWOOD, P. H., AND K. S. THOMPSON.
1960. The pectoral anatomy of *Pantodon buchholzi* Peters (a freshwater flying fish) and the related Osteoglossidae. Proc. Zool. Soc. Lond. 135:283-301.
GREENWOOD, P. H., D. E. ROSEN, S. H. WEITZMAN, AND G. S. MYERS.
1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. Bull. Am. Mus. Nat. Hist. 131:341-455.
GREGORY, W. K.
1933. Fish skulls: A study of the evolution of natural mechanisms. Trans. Am. Philos. Soc. 23:75-481. [Reissue 1959, Eric Lundberg, Laurel, Fla., seen.]
HARRINGTON, R. W., JR.
1955. The osteocranium of the American cyprinid fish, *Notropis bifrenatus*, with an annotated synonomy of teleost skull bones. Copeia 1955:267-290.
HOUDE, E. D., AND T. POTTHOFF.
1976. Egg and larval development of the sea bream *Archosargus rhomboidalis* (Linnaeus): Pisces, Sparidae. Bull. Mar. Sci. 26:506-529.
HUBBS, C. L., AND K. F. LAGLER.
1958. Fishes of the Great Lakes Region. Rev. ed. Cranbrook Inst. Sci. Bull. 26, 213 p.
JOHNSON, G. D.
1975. The procurrent spur: an undescribed perciform caudal character and its phylogentic implications. Occas. Pap. Calif. Acad. Sci. 121, 23 p.
1978. Limits and relationships of the Lutjanidae and associated families. Ph.D. Thesis, Univ. California, San Diego, 211 p.
JORDAN, D. S., AND B. W. EVERMANN.
1896. The fishes of North and Middle America. U.S. Natl. Mus. Bull. 47:951-953.
KENDALL, A. W., JR.
1976. Predorsal and associated bones in serranid and grammistid fishes. Bull. Mar. Sci. 26:585-592.
KISHINOUYE, K.
1923. Contributions to the comparative study of the so-called scombroid fishes. J. Coll. Agric., Imp. Univ. Tokyo 8:293-475.
KOJIMA, S.
1960. Fishing for dolphins in the western part of the Japan Sea V. Species of fishes attracted to bamboo rafts. Bull. Jpn. Soc. Sci. Fish. 26:379-382.
1961. Studies on fishing conditions of dolphin, *Coryphaene hippurus* L., in the western region of the Sea of Japan III. On food contents of the dolphin. Bull. Jpn. Soc. Sci. Fish. 27:625-629.
1963a. Studies on fishing conditions of the dolphin, *Coryphaena hippurus* L., in the western region of the Sea of Japan VII. Relationship between the stomach contents and the pelagic fauna of juveniles. Bull. Jpn. Soc. Sci. Fish. 29:407-414.
1963b. Studies on fishing conditions of the dolphin, *Coryphane hippurus* L., in the western region of the Japan Sea–VIII. Comparison of juvenile fish fauna in the sea and in the stomachs of dolphin. Bull. Jpn. Soc. Sci. Fish. 29:507-513.
1964. On the distribution of the dolphin, *Coryphaena hippurus* L., in the Pacific Ocean and the Indian Ocean. Bull. Jpn. Soc. Sci. Fish. 30:472-477.
KRAMER, D.
1960. Development of eggs and larvae of Pacific mackerel and distribution and abundance of larvae 1952-56. U.S. Fish Wildl. Serv., Fish. Bull. 60:393-438.
LINDSEY, C. C.
1955. Evolution of meristic relations in the dorsal and anal fins of teleost fishes. Trans. R. Soc. Can. 49, Ser. 3, Sect. 5:35-49.
LUNDBERG, J. G., AND J. N. BASKIN.
1969. The caudal skeleton of the catfishes, order Siluriformes. Am. Mus. Novit. 2398, 49 p.
MAGO LECCIA, F.
1958. The comparative osteology of the scombroid fishes of the genus *Scomberomorus* from Florida. Bull. Mar. Sci. Gulf Caribb. 8:299-341.

MILLER, G. L., AND S. C. JORGENSON.
1973. Meristic characters of some marine fishes of the western Atlantic Ocean. Fish. Bull., U.S. 71:301-313.

MITO, S.
1960. Egg development and hatched larvae of the common dolphin-fish, *Coryphaena hippurus* Linné. Bull. Jpn. Soc. Sci. Fish. 26:223-226.

MONOD, T.
1968. Le complexe urophore des poissons téléostéens. Mém. Inst. Fondam. Afr. Noire 81, 705 p.

MORROW, J. E.
1954. Data on dolphin, yellowfin tuna and little tuna from East Africa. Copeia 1954:14-16.

NICHOLS, J. T.
1909. A note on the dolphins (*Coryphaena equisetis* and *Coryphaena hippurus*). Bull. Am. Mus. Nat. Hist. 26: 131-133.

NURSALL, J. R.
1963. The hypurapophysis, an important element of the caudal skeleton. Copeia 1963:458-459.

NYBELIN, O.
1963. Zur Morphologie und Terminologie des Schwanzskelettes der Actinopterygier. Ark. Zool., Ser. 2, 15: 485-516.

PATTERSON, C.
1968. The caudal skeleton in Mesozoic acanthopterygian fishes. Bull. Br. Mus. (Nat. Hist.) Geol. 17:49-102.

PEW, P.
1957. Occurrence of young dolphin, *Coryphaena hippurus*, in a Texas Bay. Copeia 1957:300.

POTTHOFF, T.
1971. Observations on two species of dolphin (*Coryphaena*) from the tropical mid-Atlantic. Fish. Bull., U.S. 69: 877-879.
1974. Osteological development and variation in young tunas, genus *Thunnus* (Pisces, Scombridae), from the Atlantic Ocean. Fish. Bull., U.S. 72:563-588.
1975. Development and structure of the caudal complex, the vertebral column, and the pterygiophores in the blackfin tuna (*Thunnus atlanticus*, Pisces, Scombridae). Bull. Mar. Sci. 25:205-231.

POTTHOFF, T., W. J. RICHARDS, AND S. UEYANAGI.
1980. Development of *Scombrolabrax heterolepis* (Pisces, Scombrolabracidae) and comments on familial relationships. Bull. Mar. Sci. 30:329-357.

ROSE, C. D., AND W. W. HASSLER.
1968. Age and growth of the dolphin, *Coryphaena hippurus* (Linnaeus), in North Carolina waters. Trans. Am. Fish. Soc. 97:271-276.
1974. Food habits and sex ratios of dolphin *Coryphaena hippurus* captured in the western Atlantic Ocean off Hatteras, North Carolina. Trans. Am. Fish. Soc. 103: 94-100.

ROTHSCHILD, B. J.
1964. Observations on dolphins (*Coryphaena* spp.) in the central Pacific Ocean. Copeia 1964:445-447.

SAKSENA, V. P., AND W. J. RICHARDS.
1975. Description of eggs and larvae of laboratory-reared white grunt, *Haemulon plumieri* (Lacépède) (Pisces, Pomadasyidae). Bull. Mar. Sci. 25:523-536.

SCHUCK, H. A.
1951. Notes on the dolphin (*Coryphaena hippurus*) in North Carolina waters. Copeia 1951:35-39.

SHCHERBACHEV, YU. N.
1973. The biology and distribution of the dolphins (Pisces, Coryphaenidae). J. Ichthyol. 13:182-191.

SMITH, C. L., AND R. M. BAILEY.
1961. Evolution of the dorsal-fin supports of percoid fishes. Pap. Mich. Acad. Sci. Arts Lett. 46:345-363.

SPRINGER, V. G.
1968. Osteology and classification of the fishes of the family Blenniidae. U.S. Natl. Mus. Bull. 284, 85 p.

SPRINGER, V. G., AND T. H. FRASER.
1976. Synonymy of the fish families Cheilobranchidae (= Alabetidae) and Gobiesocidae, with descriptions of two new species of *Alabes*. Smithson. Contrib. Zool. 234, 23 p.

SPRINGER, V. G., AND W. C. FREIHOFER.
1976. Study of the monotypic fish family Pholidichthyidae (Perciformes). Smithson. Contrib. Zool. 216, 43 p.

STARKS, E. C.
1930. The primary shoulder girdle of the bony fishes. Stanford Univ. Publ. Biol. Sci. 6:147-240.

SWINNERTON, H. H.
1905. A contribution to the morphology and development of the pectoral skeleton of teleosteans. Q. J. Microsc. Sci., New Ser., 49:363-382.

TAKAHASHI, M., AND K. MORI.
1973. Studies on relative growth in body parts compared in *Coryphaena hippurus* and *C. equiselis*, and notes on gonadal maturation in the latter species. [In Jpn., Engl. summ.] Bull. Far Seas Fish. Res. Lab. (Shimizu) 8:79-113.

TAYLOR, W. R.
1967. An enzyme method of clearing and staining small vertebrates. Proc. U.S. Natl. Mus. 122 (3596), 17 p.

TIBBO, S. N.
1962. New records for occurrence of the white-tip shark, *Pterolamiops longimanus* (Poey), and the dolphin, *Coryphaena hippurus* L., in the northwest Atlantic. J. Fish. Res. Board Can. 19:517-518.

VOSS, N. A.
1954. The postlarval development of the fishes of the family Gempylidae from the Florida Current. I. *Nesiarchus* Johnson and *Gempylus* Cuv. and Val. Bull. Mar. Sci. Gulf Caribb. 4:120-159.

WEITZMAN, S. H.
1962. The osteology of *Brycon meeki*, a generalized characid fish, with an osteological definition of the family. Stanford Ichthyol. Bull. 8, 77 p.
1974. Osteology and evolutionary relationships of the Sternoptychidae, with a new classification of stomiatoid families. Bull. Am. Mus. Nat. Hist. 153:327-478.

WILLIAMS, F.
1953. Catches of *Coryphaena hippurus* (L) in the western Indian Ocean. Nature (Lond.) 171:703-704.

WILLIAMS, F., AND B. S. NEWELL.
1957. Notes on the biology of the dorade or dolphin-fish (*Coryphaena hippurus*) in east African waters. East Afr. Agric. For. J. (Kenya) 23:113-118.

LARVAL DEVELOPMENT OF *EUPHAUSIA EXIMIA* (CRUSTACEA: EUPHAUSIACEA) WITH NOTES ON ITS VERTICAL DISTRIBUTION AND MORPHOLOGICAL DIVERGENCE BETWEEN POPULATIONS

MARGARET D. KNIGHT[1]

ABSTRACT

Larval development of *Euphausia eximia* includes the following stages: nauplius I-II, metanauplius, calyptopis I-III, and furcilia I-VI. The larvae are similar to those of congener *E. gibboides* but differ in both morphological detail and timing of developmental events.

A comparison of larvae of *E. eximia* from across the species' range showed significant differences in morphology between forms from the California Current terminus off Baja California and from the South Equatorial and Peru Currents. This variation may be evidence of genetic divergence between populations and perhaps indicates that the oxygen-deficient warm waters of the eastern tropical Pacific form an effective barrier between reproductive centers of the species. Significant differences in morphology were found as well during a preliminary survey of adults; the southern limit of the northern form of *E. eximia* was about latitude 2° north.

The vertical distribution of larval stages in day and night samples from two locations off Baja California and one in the South Equatorial Current showed development of diurnal vertical migration in the second half of the furcilia phase after acquisition of the full complement of setose abdominal pleopods. A "reverse" migration pattern was seen among calyptopes at two stations with the majority of larvae occurring in the surface stratum during the day and below the surface layer at night; larvae at the third station were found, both day and night, in the surface stratum until the onset of vertical migration. Variation in growth rate between areas within the range of each population may be correlated with relative abundance of food and duration of stay in food-rich surface waters.

Euphausia eximia Hansen is endemic to the eastern tropical Pacific, ranging from lat. 32°-34° N to 30° S and with areas of relative abundance in waters of the California Current terminus off Baja California and the Gulf of California, in the South Equatorial Current, and in the Peru Current (Brinton 1962; Antezana-Jeréz 1978). In a recent study of the horizontal and vertical distribution of euphausiids along a transect from ca. lat. 23° N, long. 115° W to lat. 3° S, long. 88° W, Brinton (1979) observed that *E. eximia* occurred sparsely between lat. 11° and 20° N but achieved high densities in the productive zones marginal to the oxygen-deficient portion of the eastern tropical Pacific. He noted that "Reproduction, as determined by presence of larvae, was not observed between 2° and 20° N; occurrences of juvenile and adult *E. eximia* in this zone, therefore, appear due to meridional advection from the northern (21° to 25° N) and equatorial population centers." This agreed with earlier observations of *E. eximia* in these areas (Brinton 1962).

Within the genus *Euphausia*, *E. eximia* is most closely related in adult morphology to *E. americana*, an Atlantic species, and to *E. krohnii*, found in both the Atlantic and Mediterranean (Mauchline and Fisher 1969). The larvae of *E. krohnii* have been described (Frost 1934; Casanova 1974) but those of *E. americana* have not yet been identified. The literature on larval development within the Euphausiacea has been reviewed by Gopalakrishnan (1973).

The purpose of this paper is to describe the larval development of *E. eximia* in the reproductive area of the California Current terminus population, to note the differences observed in morphology of larvae from the South Equatorial-Peru Current population and apparent variation within each population in rate of growth, and to provide information on the vertical distribution of larval stages.

METHODS

Larvae of *E. eximia* were sorted from preserved samples of plankton taken in the eastern Pacific (Figure 1) during Scripps Institution of Oceanog-

[1]Scripps Institution of Oceanography, University of California, La Jolla, CA 92093.

Manuscript accepted December 1979.
FISHERY BULLETIN: VOL. 78, NO. 2, 1980.

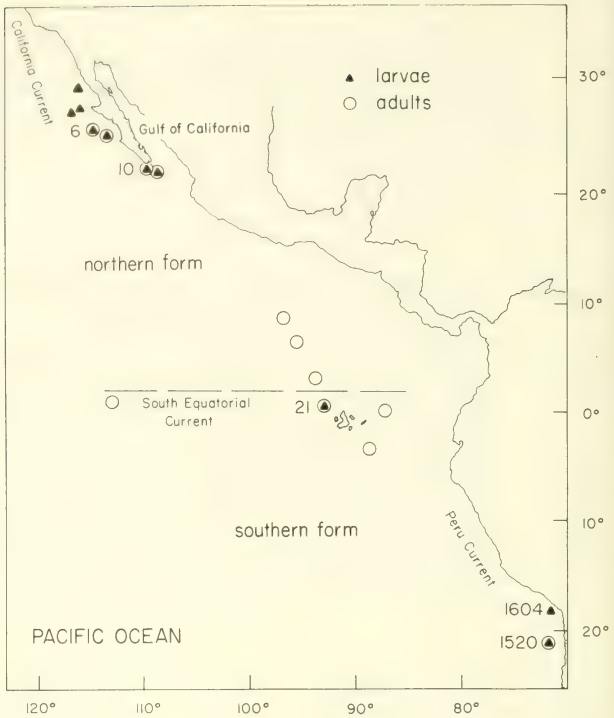


FIGURE 1.—Occurrence of northern and southern forms of *Euphausia eximia* in plankton samples from the eastern Pacific Ocean; Krill Expedition station numbers locate samples in which vertical distribution and growth of larvae were studied.

raphy Expeditions Krill, Aries, and Muddauber, and CalCOFI Cruise 5804. They were identified from an area off western Baja California in which *E. eximia* is consistently abundant and where closely related species (*E. mutica* and *E. recurva*), whose larvae we have identified, are rarely, if ever, present (Brinton 1967). At three locations (Stations 6, 10, and 21) larvae were counted as well in separate day and night series of tows taken across eight strata above 500 m on Krill Expedition (Brinton 1979) to investigate patterns of vertical distribution.

Larvae from each sample were grouped by size, information from length-frequency histograms, and degree of morphological differentiation into developmental stages which, to furcilia IV, were discrete and assumed to be separated by one molt. Furcilia V-VI and juvenile I were also presumed to be one intermolt although individual variation in growth and morphogenesis made boundaries less distinct. Altogether 2,210 individuals were measured and 347 dissected for study of appendages. Measurements were made with an ocular micrometer; the method was the same as that used in studies of species of the *E. gibboides* group (Knight 1975, 1978). In the comparison of growth rate between areas within each population larvae from Stations 1520 and 1604 were treated as one sample. Larvae were dissected in glycerine and at least 10 specimens of each stage were examined in detail. In the description of larval stages, the usual setation or condition noted is given in parentheses following the range observed. Drawings were prepared with the drawing attachment of a Wild M20 Microscope.[2]

The nomenclature used to describe larval morphology was modified from the studies cited above with respect to the mandible. It appears appropriate to refer to the dentate process near incisor

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

teeth of the right mandible as the lacinia mobilis (Weigmann-Haass 1977; Hessler[3]). In species of *Euphausia* I have examined in detail (*E. gibboides*, *E. sanzoi*, *E. fallax*, *E. pacifica*), in *Nematoscelis difficilis* (Gopalakrishnan 1973), and *Nyctiphanes couchii* (Le Roux 1976), the lacinia mobilis appeared only on the right mandible; it was found on the left mandible of *E. hanseni* by Weigmann-Haass (1977). Leg 1 is referred to as maxilliped through the furcilia phase.

Adults were sorted from a set of samples (Figure 1) for preliminary exploration of morphological differences between populations of *E. eximia*. The animals were sexed, measured to the nearest millimeter, and the armature of telson and inner process of segment 2 of antennular peduncle were inspected.

Gravid females of *E. eximia*, captured in nighttime plankton tows with a 1 m net from 200 m to the surface near Santa Catalina Island, were cultured aboard ship using the methods described by Lasker and Theilacker (1965). Larvae hatched from eggs spawned by one of the females were held through calyptopis I to confirm identification of early larval stages.

RESULTS

Observations of Reared Animals

Two gravid females spawned on the night of capture; they were 25.7 and 26.6 mm total length (TL) and shed 154 and 196 eggs. Their ovaries were blue before spawning and the embryos of the newly laid eggs were pale blue; the color faded before hatch. Of 154 eggs allowed to develop, 90% hatched and, at 17°-19° C room temperature, the duration of early larval stages was approximately as follows: 24 h for the egg; 24 h for nauplius I and II together; 48 h for the metanauplius. The first calyptopis appeared on the fourth day after spawn. These stages encounter similar temperatures in the surface waters off Baja California.

The spent female molted 6 days after spawning without shedding more eggs; a spermatophore was not found on the preserved female or her exuvia. Three other ovigerous females survived capture and molted twice, with 4 days between molts, without spawning; each shed a spermatophore with the exuvia during the first molt and the ovaries remained blue.

Description of Larval Stages

Larval development in the California Current population (northern form) of *Euphausia eximia* included the following stages: nauplius I and II; metanauplius; calyptopis phase, three stages; furcilia phase, six stages. The stage which followed furcilia VI usually (in 92% of 53 individuals) had the adult number of spines on the telson (one terminal and two pairs posterolateral) and is referred to here as juvenile I. The observed furcilia stages are listed in Table 1 along with the development of pleopods, telson, and antenna. Measurements of the calyptopis, furcilia, and juvenile stages are given in Tables 2 and 3.

TABLE 1.—Development of pleopods, telson spines, and antenna in furcilia I-VI and juvenile I in the northern and southern forms of *Euphausia eximia*; ' = pair nonsetose pleopods, " = pair setose pleopods.

Stage	Pleopod development	Telson spines		Form of antenna	Number of larvae	
		Terminal	Posterolateral		Northern form	Southern form
Furcilia I	1'	7	3	Natatory	151	72
Furcilia II	1'4	7	3	Natatory	132	80
Furcilia III	5"	7	3	Natatory	334	104
		6	3		0	9
		5	3		1	4
		4	3		0	3
		3	3		1	5
Furcilia IV	5	6	3	Juvenile	2	0
		5	3		8	0
		4	3		16	0
		3	3		128	2
		2	3		85	5
		1	3		192	57
Furcilia V	5"	1	3	Juvenile	195	45
		1	2		0	1
Furcilia VI	5"	1	3	Juvenile	40	42
		1	2		19	25
Juvenile I	5"	1	3	Juvenile	4	0
		1	2		49	47

TABLE 2.—Measurements (millimeters) of metanauplius and calyptopis I-III in the northern form of *Euphausia eximia*.

Stage	Total length	Carapace length	Carapace width	Telson width
Metanauplius, n = 123:				
Range	0.46-0.51	—	0.33-0.39	—
Mean	0.49		0.35	
SD	0.01		0.01	
Calyptopis I, n = 127:				
Range	0.97-1.09	0.59-0.67	0.36-0.44	0.158-0.186
Mean	1.03	0.62	0.40	0.170
SD	0.02	0.02	0.01	0.006
Calyptopis II, n = 140:				
Range	1.58-1.76	0.75-0.81	0.40-0.46	0.195-0.242
Mean	1.67	0.78	0.43	0.224
SD	0.04	0.02	0.02	0.008
Calyptopis III, n = 140:				
Range	2.20-2.55	0.89-0.99	0.50-0.61	0.242-0.279
Mean	2.36	0.94	0.56	0.260
SD	0.06	0.02	0.02	0.009

[3]Robert R. Hessler, Professor of Oceanography, Scripps Institution of Oceanography, Univ. Calif., La Jolla, CA 92037, pers. commun. July 1978.

Although there is variation in timing of events with respect to stage, the form, setation, and development of appendages are very similar in larvae of congeners *E. gibboides* and *E. eximia*. The descriptions with figures of *E. gibboides* larvae (Knight 1975) may be consulted for morphology and development of appendages of *E. eximia* which are figured and discussed in detail here only when necessary to contribute information specific to *E. eximia*. The setations of maxillule, maxilla, and pleopods in larvae of *E. eximia* are given in Tables 4, 5, and 6.

TABLE 3.—Measurements (millimeters) of furcilia I-VI and juvenile I in the northern form of *Euphausia eximia*.

Stage	Total length	Carapace length	Telson width
Furcilia I, n = 151:			
Range	2.87-3.19	0.81-0.87	0.232-0.270
Mean	3.02	0.84	0.250
SD	0.07	0.02	0.009
Furcilia II, n = 132:			
Range	3.41-3.84	0.89-1.01	0.195-0.232
Mean	3.59	0.94	0.219
SD	0.09	0.02	0.009
Furcilia III, n = 183:			
Range	3.84-4.46	0.97-1.13	0.158-0.214
Mean	4.13	1.05	0.188
SD	0.12	0.03	0.010
Furcilia IV, n = 269:			
Range	4.08-4.97	1.07-1.25	0.149-0.195
Mean	4.60	1.16	0.167
SD	0.15	0.03	0.008
Furcilia V, n = 158:			
Range	4.52-5.66	1.13-1.39	0.121-0.177
Mean	5.13	1.26	0.153
SD	0.23	0.05	0.008
Furcilia VI, n = 58:			
Range	5.09-6.06	1.19-1.45	0.112-0.158
Mean	5.55	1.34	0.138
SD	0.23	0.06	0.009
Juvenile I, n = 53:			
Range	5.45-6.79	1.35-1.64	0.112-0.149
Mean	6.15	1.49	0.131
SD	0.32	0.07	0.007

EGGS.—Perivitelline space relatively small, 50 spawned eggs with the following measurements: Outer diameter, 0.38-0.46 mm; mean, 0.45 mm; SD, 0.02 mm. Perivitelline space, 0.03-0.07 mm; mean, 0.06 mm; SD, 0.01 mm. Eighty-five eggs from the plankton differed slightly: Outer diameter, 0.40-0.48 mm; mean, 0.45 mm; SD, 0.01 mm. Perivitelline space, 0.03-0.07 mm; mean, 0.05 mm; SD, 0.01 mm.

NAUPLIUS I AND II.—Body ovoid, as figured for *E. gibboides*, with one pair long posterior spines in nauplius I and a second short outer pair in nauplius II; both stages with 3 pairs of functional appendages—antennule, antenna, and mandible. Seven hatched nauplius I larvae with the following dimensions: Length, 0.38-0.41 mm; mean, 0.39 mm; SD, 0.02 mm. Width, 0.25-0.27 mm; mean, 0.26 mm; SD, 0.01 mm.

TABLE 4.—Development of maxillule in the northern form of *Euphausia eximia*; exopod with 4 setae and endopod with 2 medial and 3 terminal setae in all stages; () = usual condition.

Stage	Endopod		Basal endite setae		Coxal endite setae	Pseudexopod	
	Segments	Lateral seta	Medial	Proximal		Presence	Anterior seta
Calyptopis I	2	0	3	0	7	–	0
Calyptopis II-III	2	0	5	0	7	–	0
Furcilia I	2	0	6-7(7)	0	8	–	0
Furcilia II	2	0	7	0-1(1)	8	–	0
Furcilia III	2	0	9	1	8-9(8)	–	0
Furcilia IV	1-2	0-1(0)	8-10(9)	1	8-9(9)		0
Furcilia V	1	1	8-10(9-10)	1-2(1)	8-9(9)	–/+(+)	0
Furcilia VI	1	1	9-13(10)	1-2	9-10(9)	+	0
Juvenile I	1	1	10-12(10-11)	1-2(2)	9-11(10)	+	0-1

TABLE 5.—Setation of maxilla in the northern form of *Euphausia eximia*; medial lobe five with 3 setae in all stages; () = usual condition.

Stage	Exopod	Endopod	Medial lobes			
			1	2	3	4
Calyptopis I-III	1	3	8	4	4	4
Furcilia I	1	3	8	4	4-5 (5)	4
Furcilia II	1	3	8	4	4-5 (5)	4
Furcilia III	1	3	8	4	5-6 (5)	4-5 (4)
Furcilia IV	1	3	8	4-6 (4)	5-6 (6)	5
Furcilia V	1	3	8	4-6 (5-6)	6-7 (6)	5-6 (5)
Furcilia VI	1-3 (1-2)	3-4	8	5-6 (6)	6-7 (6)	5-6 (6)
Juvenile I	2-6 (2-5)	3-6 (4)	8-9 (8)	6	6-9 (7)	6-7 (6)

METANAUPLIUS (FIGURES 2A, 3A).—Rostral hood of carapace fringed with spines, 3 pairs on anterior margin relatively long, a fourth anterolateral pair sometimes somewhat longer than surrounding spines; usually 3 shorter spines between medial pair of long spines, tiny spines rarely interspersed; other small spines variable in number. Dorsal crest high, rounded, with 2 small spines (frequently broken or bent in preserved

TABLE 6.—Setation of pleopods in the northern form of *Euphausia eximia*; () = usual condition.

	Pleopod I		Pleopod 2		Pleopod 3		Pleopod 4		Pleopod 5	
Stage	Exopod	Endopod	Exopod	Endopod	Exopod	Endopod	Exopod	Endopod	Exopod	Endopod
Furcilia I	0	0	—	—	—	—	—	—	—	—
Furcilia II	6	1	0	0	0	0	0	0	0	0
Furcilia III	6-8(6)	2	6	1	6	1	6	1	6	1
Furcilia IV	7-8(8)	2-4(3-4)	8-9(8)	2-3(2)	8	2-3(2)	7-8(8)	2-3(2)	6-8(7-8)	2
Furcilia V	8-10(9)	4-6(4)	8-10(9)	4-5(4)	8-10(9)	3-5(4)	8-10(9)	4	7-9(8)	3-4(4)
Furcilia VI	9-11(10)	4-6(6)	9-11(10)	4-6(6)	9-11(10)	5-6	9-11(9-10)	4-6(5-6)	8-10(8-9)	4-5(4)
Juvenile I[1]	10-13(11)	5-7(6)	11-12(11)	6-7(6)	11-12(11)	6-7(6)	10-12(11)	6-7(6)	9-11(9)	4-6(5)

[1]In juvenile I, 11, 13, and 7% of pleopods 1, 2, and 3 with 1 seta proximal to appendix interna on endopod in 30 individuals.

specimens). Small pair of papillae on anterior margin of body beneath carapace; Fraser (1936) described papillae as frontal sensory organs.

Antennule and antenna functional, mandible reduced, buds of maxillule, maxilla, and maxilliped present.

Abdomen short, posterior margin with 5 pairs of spines; relatively long third pair articulated with telson, shorter spines fused. The long spine is plumose in *E. gibboides* but appears nearly smooth (with tiny serrations sometimes visible) in *E. eximia*.

CALYPTOPIS I (FIGURES 2B, 3B).—Rostral hood of carapace fringed with spines curving medially on anterior margin and posteriorly on posterolateral curve of hood; posterior margin of carapace produced into small dorsal spine; dorsal crest without spines. Striated body of photophore visible in developing compound eye, ocular papillae situated medially slightly below anterior margin of eye.

Mandibles (Figure 4a) with asymmetrical median armature and with anterolateral process but without lateral knob seen in species of the *E. gibboides* group (lateral knob is not found in any stage of *E. eximia*); anterolateral process, representing palp (Gurney 1942), decreases in size until furcilia V.

Maxillule and maxilla functional.

Maxilliped (Figure 5a) with form and setation as in *E. gibboides*: coxa with 4 setae on inner margin and 1 seta on posterior face; basis with 5 setae on inner margin and 1 distal submarginal seta, 1 marginal seta noticeably stout; endopod 2-segmented, proximal segment with 3 setae, 2 marginal and 1 submarginal, 1 marginal seta small and stout, distal segment with 4 terminal setae; exopod with 4 terminal setae and 1 lateral seta near articulation with basis. In *E. gibboides* the stout setae of endopod segment 1 and basis are nearly equal in length.

Abdomen unsegmented.

Telson (Figure 6a) with 1 pair lateral, 3 pairs posterolateral, and 6 terminal spines, middle posterolateral spine slightly longer than other spines.

CALYPTOPIS II (FIGURES 2C, 3C).—Carapace with lateral margins of rostral hood curved ventrally around body so that in dorsal view marginal spines are visible only on anterior margin of carapace.

Maxilliped with stout seta of endopod segment 1 and basis now about equal in length, as figured for calyptopis III (Figure 5b).

Abdomen with 5 segments.

Telson (Figure 6b) with 7 terminal spines, middle posterolateral spine relatively long, armature of telson spines as in *E. gibboides*.

CALPYTOPIS III (FIGURES 2D, 3D).—Carapace still with marginal spines of rostral hood visible in dorsal view only on anterior margin which extends well beyond eyes; lateral margins with denticle. Pigment sometimes visible in developing compound eyes; ocular papillae small, set farther out on eyestalk.

Maxilliped (Figure 5b) endopod with 5 setae on terminal segment unlike species of *E. gibboides* group which retain 4 setae in this stage, coxa with 6 setae.

Abdomen with 6 segments, sixth segment with pair of biramous uropods.

FURCILIA I (FIGURES 7A, 8A).—Carapace with rectangular rostral plate fringed with marginal spines which curve toward small median spine or denticle; posterior margin with dorsal spine. Eyes movable, pigmented, with rounded contour in furcilia stages (Figure 8d) unlike lobed contour of *E. gibboides* eye.

Bud of leg 2 present.

Abdomen with one pair nonsetose pleopods on segment 1.

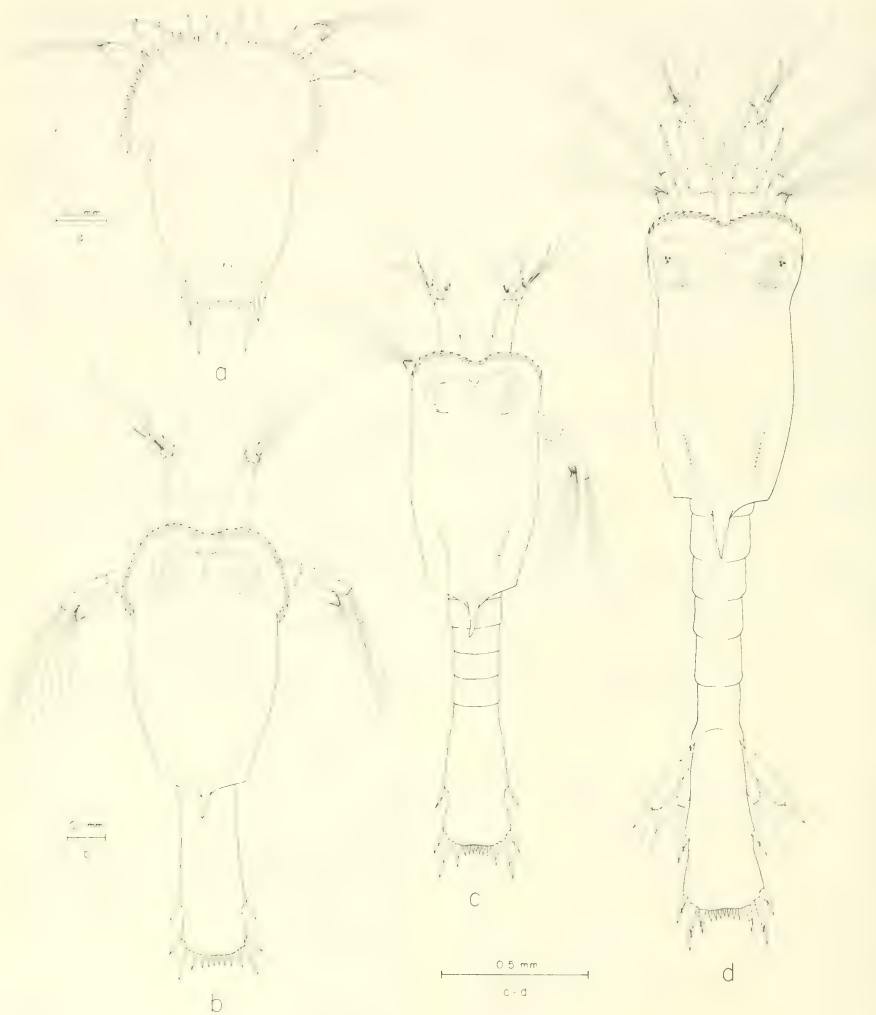


FIGURE 2.—*Euphausia eximia*, northern form, dorsal view: a, metanauplius; b-d, calyptopis I-III.

FURCILIA II (FIGURES 7B, 8B).—Carapace with narrower rostral plate and larger median spine, posterior margin without dorsal spine.

Maxilliped endopod with 5 or 6 (5) setae on distal segment.

Leg 2 endopod with 3-5 (4) segments, 1 or 2 (2) terminal setae, and variable marginal setation; exopod nonsetose; gill with two lobes; developing photophore may be visible.

Leg 3 unsegmented, nonsetose, with bud of exopod and bifid gill bud.

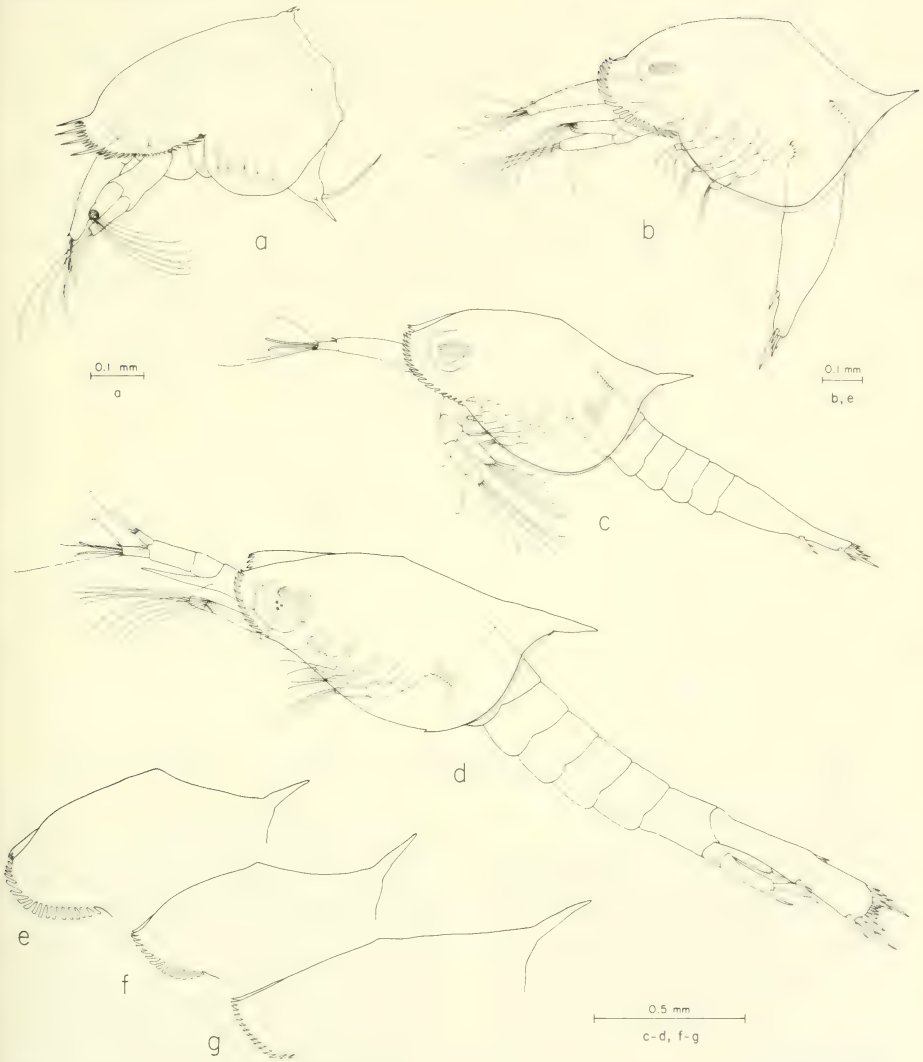


FIGURE 3.—*Euphausia eximia*, lateral view. Northern form: a, metanauplius; b-d, calyptopis I-III. Southern form: e-g, calyptopis I-III.

Buds of legs 4 and 7 sometimes present.

Abdomen with one pair setose pleopods on segment 1 and 4 pairs nonsetose pleopods on segments 2-5; photophore on segment 1 pigmented, photophore of segment 4 sometimes forming.

FURCILIA III (FIGURES 7C, 8C).—Carapace with rostrum narrower and lengthening.

Antennule with flagella lengthening, often 2-segmented; 1 of 2 aesthetes on outer ramus bifurcate distally as in *E. gibboides* furcilia III.

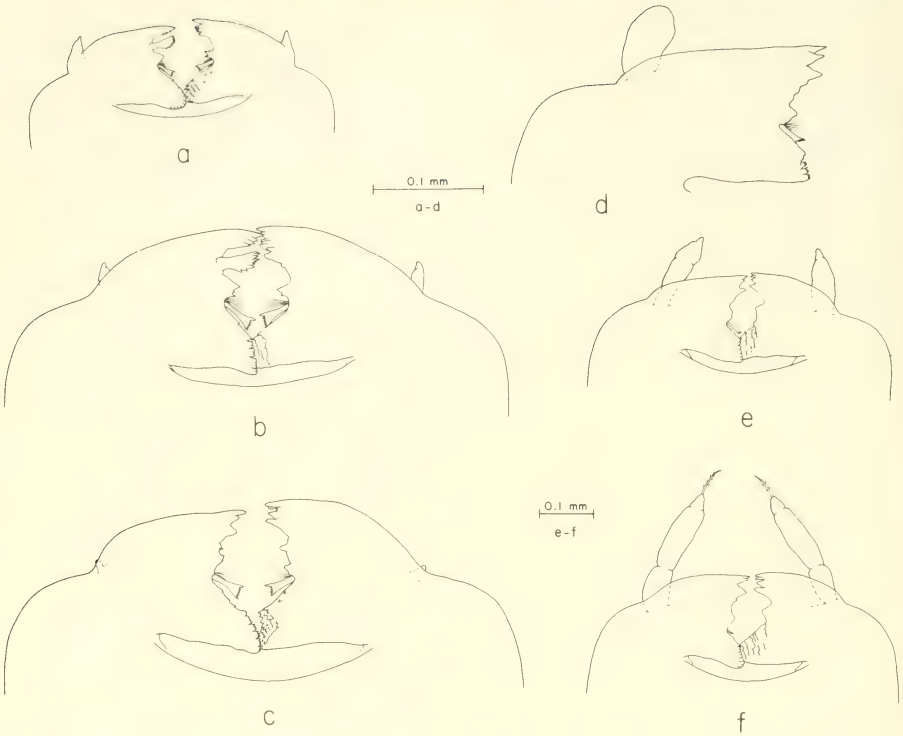


FIGURE 4.—*Euphausia eximia*, northern form. Mandible, posterior view: a, calyptopis I; b-e, furcilia III-VI; f, juvenile I.

Maxilliped endopod with 5 or 6 setae on distal segment.

Leg 2 endopod 5-segmented with more than 2 terminal setae; exopod with 2-4 (3) setae; gill sometimes with bud of third lobe; photophore pigmented.

Leg 3 endopod 5-segmented with 2 terminal setae and variable marginal setation; exopod with 0 or 1 (0) seta; gill with bud of third lobe.

Leg 4 endopod unsegmented with 0 or 1 (0) terminal seta; exopod nonsetose; gill with two lobes.

Leg 5 rudimentary, sometimes with buds of exopod and gill.

Leg 7 with bifid gill and developing photophore visible.

Bud of leg 8 sometimes present.

Abdomen with 5 pairs setose pleopods; photophores pigmented on segments 1 and 4 and forming on segment 2.

Telson (Figure 6f) still usually with 7 terminal spines and 3 pairs posterolateral spines (2 of 336 larvae varied with 3 and 5 terminal spines); telson of next instar sometimes visible beneath cuticle, the following percentages (in parentheses) of terminal spines were observed among 293 furcilia III larvae: 7(1.0), 6(0.3), 5(1.4), 4(2.4), 3(30.4), 2(15.7), 1(48.8). The setation pattern on inner margins of middle and innermost posterolateral spines differs from *E. gibboides*; the middle spine has 3 stronger spinules separated by small spinules and inner spine bears several spinules distally.

FURCILIA IV (FIGURES 7D, 9A).—Carapace with a few small spines on lateral margins of rostrum and stronger median spine.

Antennular flagella with 8 or 9 segments, one of the paired aesthetes on outer ramus no longer bifurcate.

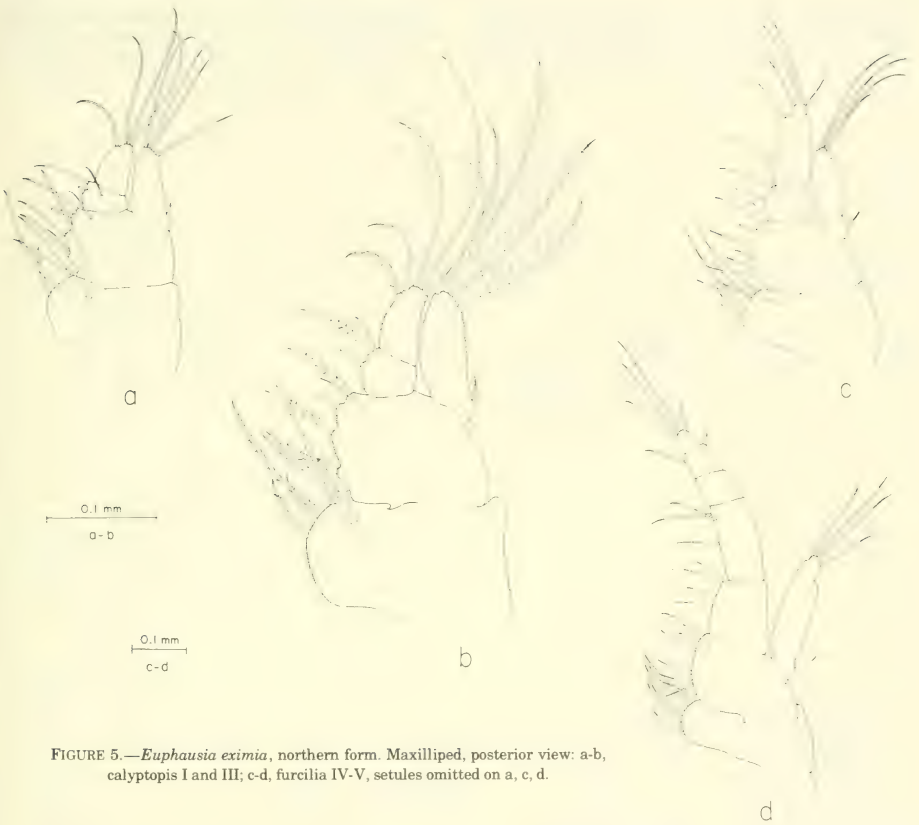


FIGURE 5.—*Euphausia eximia*, northern form. Maxilliped, posterior view: a-b, calyptopis I and III; c-d, furcilia IV-V, setules omitted on a, c, d.

Antenna (Figure 10a) modified from natatory to juvenile form, scale (exopod) with 11-13 (12) setae, flagellum (endopod) with 4-6 (4) segments, 2 or 3 (2) peduncular and 2-4 (2) flagellar.

Mandible (Figure 4c) modified with fewer, somewhat broader incisor teeth and lacinia mobilis missing or very much reduced; anterolateral process very small.

Maxilliped (Figure 5c) with 5 or 6 (6) setae on distal segments of lengthening endopod; basis and coxa with 6-8 (6-7) setae.

Leg 2 exopod with 5 or 6 (5) setae, gill with three lobes.

Leg 3 endopod with >2 terminal setae, exopod with 4-6 (5) setae; gill with three lobes, rarely with bud of fourth lobe.

Leg 4 endopod 5-segmented with 2-5 (2) terminal setae, exopod with 0-4 (0-2) setae; gill with small third lobe.

Leg 5 endopod usually unsegmented (ca. 3 segments occasionally seen) with 0-2 (0-1) terminal setae; exopod nonsetose; gill sometimes with bud of third lobe.

Leg 6 rudimentary with exopod bud and 2 or 3 gill buds.

Leg 7 with lightly pigmented photophore and three-lobed gill; leg 8 with three gill lobes.

Abdomen with photophores pigmented on segments 1, 2, and 4, and sometimes forming on segment 3.

Telson (Figure 6g) with 6-1 terminal spines and 3 pairs posterolateral spines (Table 1), 45% of 431 furcilia IV with 1 and 30% with 3 terminal spines (frequencies similar to those observed on develop-

ing telson of furcilia IV in premolt furcilia III); telson of next instar when forming beneath cuticle with 1 terminal and 3 pairs posterolateral spines. Inner margin of innermost posterolateral spine with series of strong spinules and shorter spinules interspersed. A second pair of lateral spines, or a

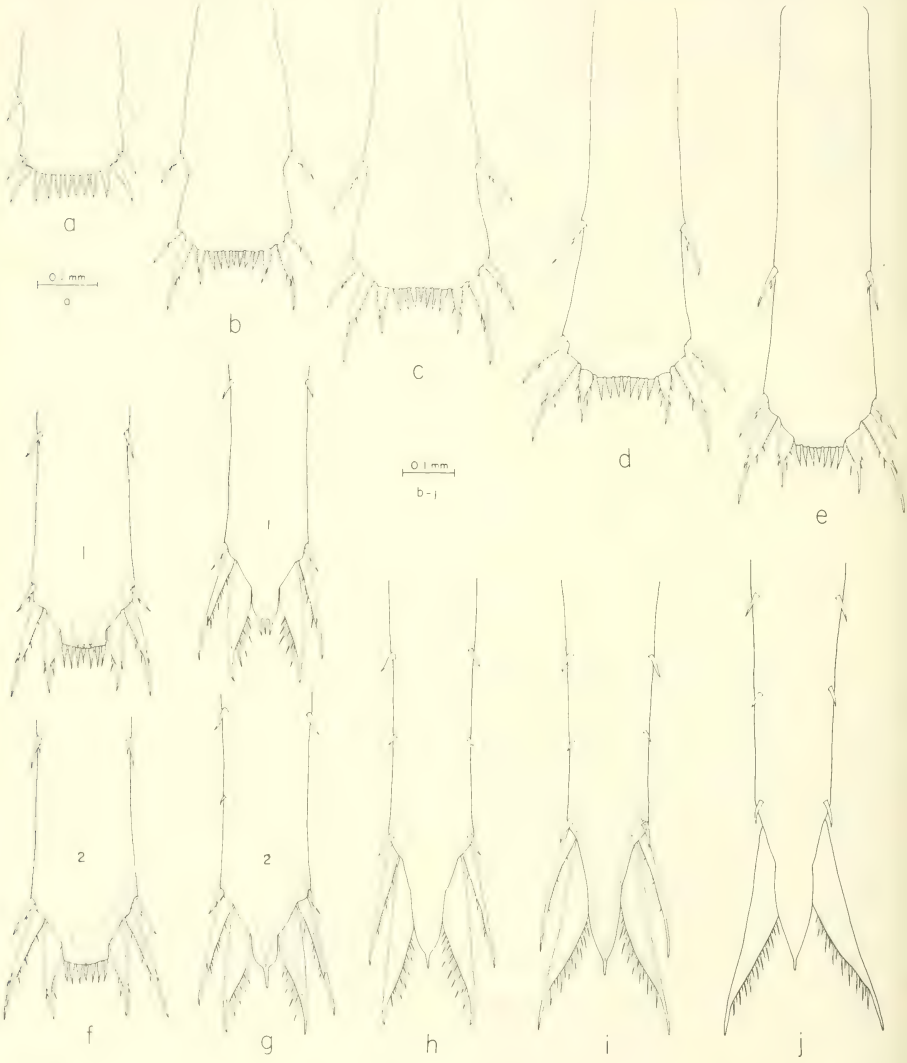


FIGURE 6.—*Euphausia eximia*, northern form. Telson, dorsal view: a-c, calyptopis I-III; d-e, furcilia I-II; f, furcilia III, 1-premolt to 3 terminal spines, 2-premolt to 1 terminal spine; g, furcilia IV, 1-with 3 terminal spines, 2-with 1 terminal spine; h-i, furcilia V-VI; j, juvenile I.

single additional spine on one side only, was found on 48% of 87 larvae examined for this feature.

FURCILIA V (FIGURES 7E, 9B).—Carapace with or without a few tiny lateral denticles on rostrum.

Antennule with lateral spine of peduncle segment 1 slightly longer than or equal to length of

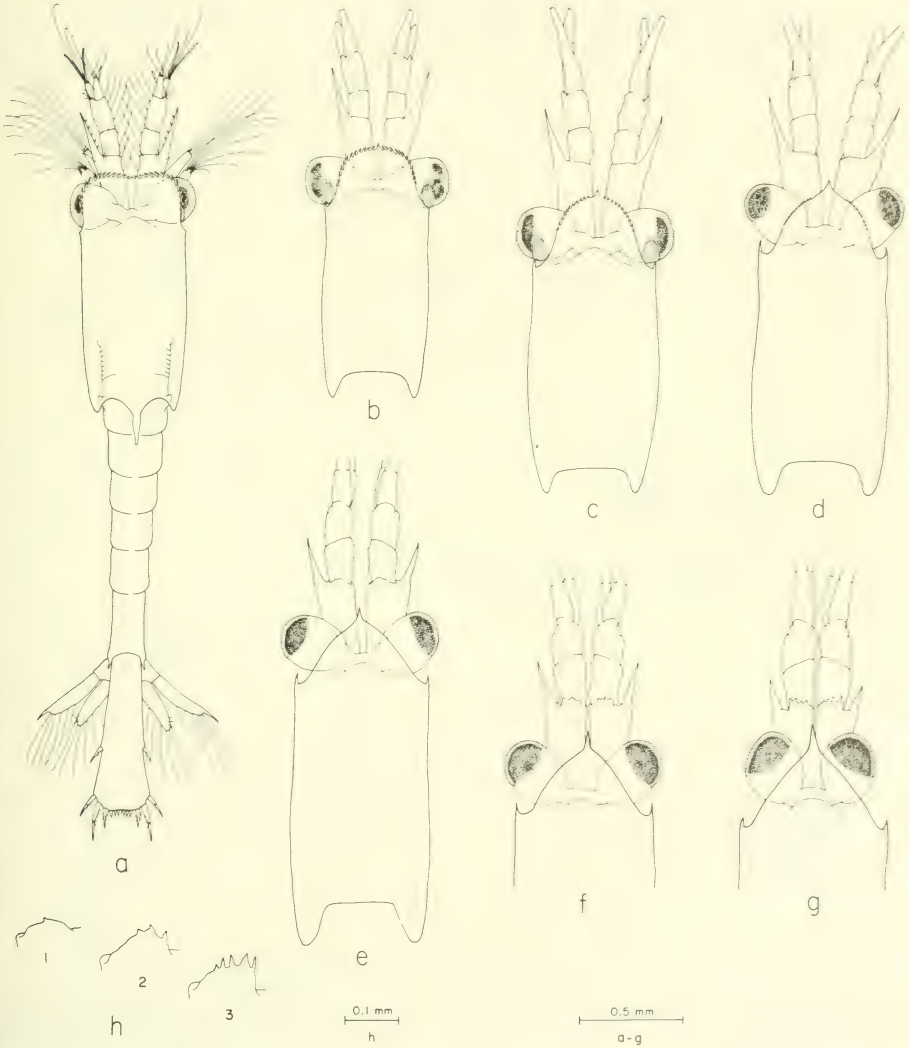


FIGURE 7.—*Euphausia eximia*, northern form, dorsal view: a-f, furcilia I-VI; g, juvenile I; h1-3, typical development of dorsal lappet on segment 1 of antennular peduncle in furcilia V-VI and juvenile I

segment 2, sometimes small variable rudiment of dorsal lappet present on segment 1 of peduncle with margin smooth or extended into 1 or 2 small knobs (Figure 7h-1); no specimens with flagella intact.

Antennal scale with 13-16 (14-15) setae and

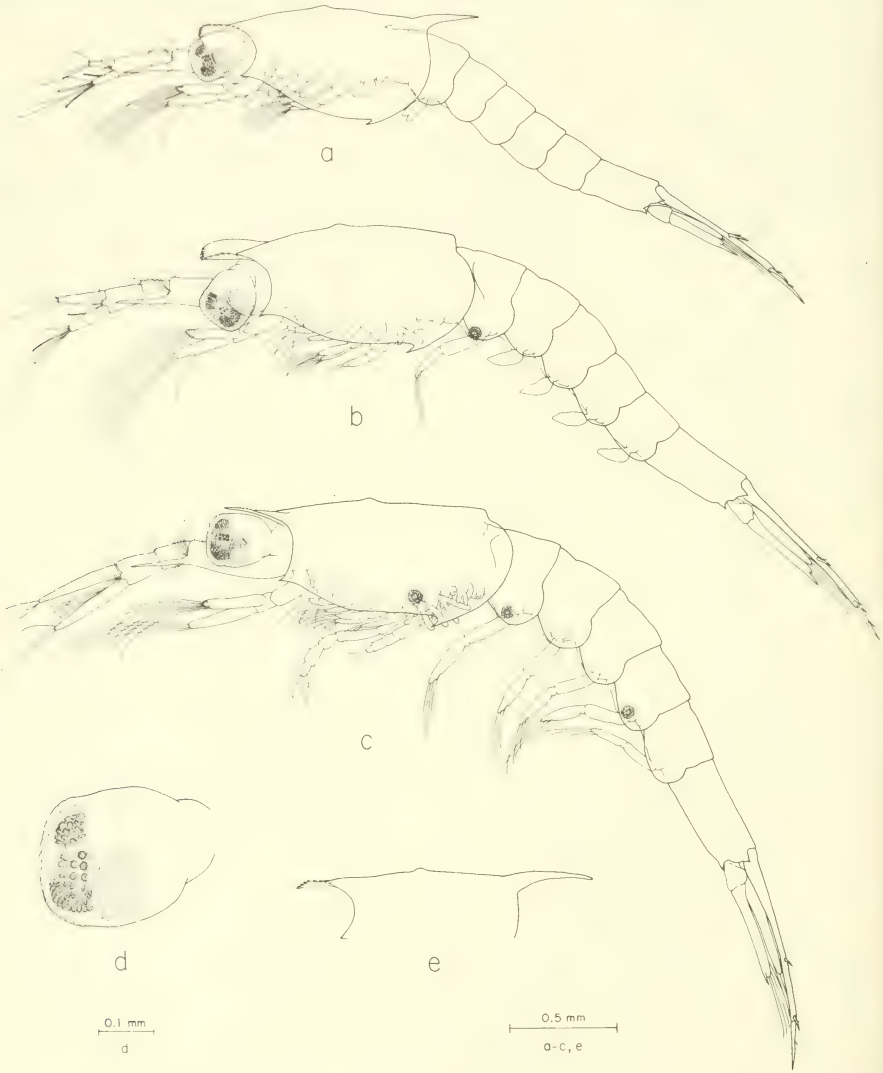


FIGURE 8.—*Euphausia eximia*, lateral view. Northern form: a-c, furcilia I-III; d, eye of furcilia II. Southern form: e, carapace of furcilia I.

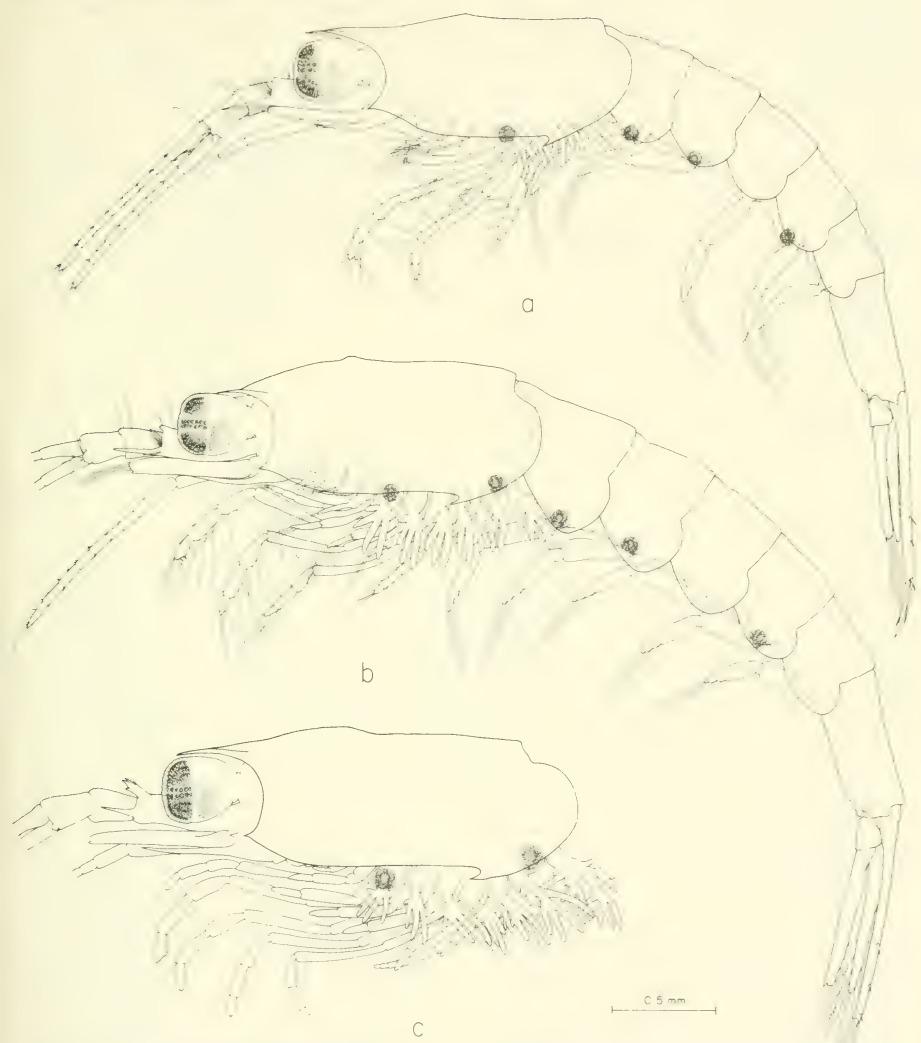


FIGURE 9.—*Euphausia eximia*, northern form, lateral view: a-b, furcilia IV-V; c, juvenile I.

flagellum usually with 12 segments, 3 peduncular and 7-10 (9) flagellar (Figure 10b).

Mandible (Figure 4d) without remnant of lacinia mobilis, palp lengthening.

Maxilliped (Figure 5d) with endopod now about equal in length to knee of leg 2, basis with 7-9 (8), and coxa with 6-8 (6) setae and usually without long seta on posterior face.

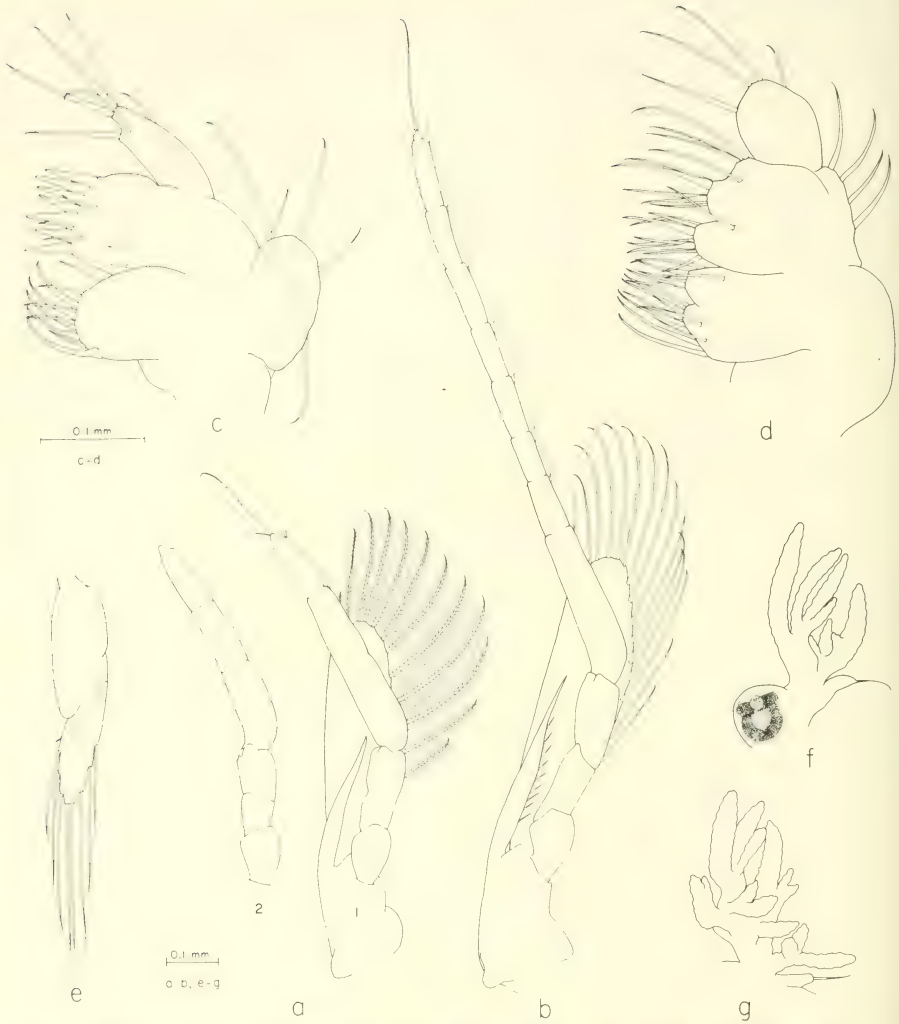


FIGURE 10.—*Euphausia eximia*, northern form. Antenna, ventral view: a 1-2, furcilia IV with variation in segmentation of endopod; b, furcilia V. Maxillule and maxilla, posterior view: c-d, juvenile I. Leg 2 exopod and legs 7-8: e-g, juvenile I (setules omitted in b-e).

Leg 2 exopod with 6 or 7 (6) setae, 1 of 28 appendages examined with additional proximal seta on inner margin common in furcilia VI and juvenile I (Figure 10e); gill sometimes with bud of fourth lobe.

Leg 3 exopod with 5-7 (6) setae, 1 of 34 appendages examined with proximal seta as on leg 2 exopod; gill sometimes with bud of fourth lobe.

Leg 4 endopod setose; exopod with 4-6 (5) setae; gill sometimes with bud of fourth lobe.

Leg 5 endopod with 4 or 5 (5) segments and 1-5 (2) terminal setae; exopod with 0-5 (0-2) setae; gill with bud of third lobe.

Leg 6 endopod unsegmented with 0 or 1 (0) terminal seta; exopod nonsetose and gill with two or three lobes.

Legs 7 and 8 with more than three gill lobes.

Abdomen with pigmented photophores on segments 1, 2, and 4, photophore on segment 3 sometimes with visible structure and some pigment.

Telson (Figure 6h) with 1 terminal and 3 pairs of posterolateral spines; telson of next instar when visible beneath cuticle with only 2 pairs posterolateral spines in 38% of 77 larvae; 97% of 71 furcilia V with 2 pairs lateral spines.

FURCILIA VI (FIGURE 7F).—Carapace with smooth lateral margins on well-developed rostrum.

Antennule with lateral spine about equal or less than length of peduncle segment 2, dorsal lappet of segment 1 with small knob or few spines (Figure 7h-2).

Antennal scale with 15-18 (16) setae; flagella no longer intact in preserved specimens.

Mandibles (Figure 4e) with palp relatively long, usually unsegmented, sometimes constricted into 2 or 3 weakly defined segments; 1 of 18 furcilia VI with 1 terminal seta on 2-segmented palp; slender terminally dentate plate near molar area of each mandible reduced, sometimes missing on left mandible.

Maxilliped continues to lengthen to juvenile form, endopod 5-segmented and setose, exopod still with 1 proximal and 4 distal setae, coxa without long seta on posterior face.

Leg 2 exopod with 6-8 (6-7) setae, 14 of 17 appendages examined with additional proximal seta on inner margin (Figure 10e); gill with four lobes.

Leg 3 exopod with 6-8 (6) setae, 22 of 24 appendages with proximal seta; gill with four lobes.

Leg 4 exopod with 6 or 7 (6) setae, 4 of 21 appendages with proximal seta; gill with four lobes.

Leg 5 endopod 5-segmented and setose; exopod with 4-6 (5) setae; gill with four lobes.

Leg 6 endopod with 0-5 (0-3) segments and 0-2 (1) terminal setae; exopod with 0-3 (0) setae; gill with four or more lobes.

Legs 7 and 8 with branching gill lobes, rudiment of leg 7 sometimes with terminal seta (Figure 10f).

Abdomen with photophores pigmented on segments 1-4.

Telson (Figure 6i) with 3 or 2 (in 32% of 59 larvae) pairs of posterolateral spines, developing telson of next instar when visible beneath cuticle with 2 pairs posterolateral spines in 18 of 19 larvae; 94% of 52 furcilia VI with 2 pairs of lateral spines.

JUVENILE I (FIGURES 7G, 9C).—Carapace with lengthening rostrum.

Antennule with lateral spine from slightly less than to about one-third the length of peduncle segment 2, lappet with 3-6 spines (Figure 7h-3).

Antennal scale with 16-19 (18) setae.

Mandibles (Figure 4f) with palp usually three-segmented, sometimes with 1 terminal seta and 0-3 lateral setae on segment 2, median armature as in furcilia VI.

Maxillule without or with seta on anterior margin of pseudexopod and maxilla with increasing numbers of setae on endopod and exopod (Tables 4, 5; Figure 10 c-d).

Leg 1 (maxilliped) exopod with 4-7 (4) setae.

Leg 2 exopod (Figure 10e) with 6-8 (8) setae, all with additional proximal seta on inner margin; gill with four lobes.

Leg 3 exopod with 6-8 (8) setae plus proximal seta on inner margin; gill with four lobes.

Leg 4 exopod with 6-8 (6-7) setae, 12 of 20 appendages with proximal seta; gill with four lobes.

Leg 5 exopod with 5-8 (6-7) setae, 3 of 17 appendages with proximal seta; gill with four lobes.

Leg 6 endopod with 4 or 5 (5) segments and 2-4 (2) terminal setae; exopod with 2-6 (2-3) setae; gill many branched.

Legs 7 and 8 (Figure 10f-g) rudiments each with terminal seta and ramified gills.

Telson (Figure 6j) usually with 2 pairs posterolateral and 2 pairs lateral spines (in 92% and 98% of 53 larvae).

In *E. eximia*, as in *E. gibboides*, the reduction in number of terminal telson spines appears not to be a reliable single guide to recognition of developmental stages in furcilia IV-VI but rather only one of a group of features that characterize these stages. Furcilia IV of *E. eximia*, as delimited in this study, had a variable number of terminal spines which overlapped with the number of terminal telson spines in furcilia III and V. Furcilia IV differed from furcilia III, however, in the following features: modification of both antenna and mandible; segmentation of antennular flagellum; setation of exopods of legs 2 and 3; setation and segmentation of leg 4 endopod; and setation of

pleopods 2-5. Furcilia IV was separated from furcilia V by the segmentation of antennal flagella, maxilliped endopod, and leg 5 endopod; and endopod setation of pleopods 2-5, with small overlap on pleopod 3 only. Grouping of stages by terminal telson spine number would not be supported by these characters and if, for instance, all larvae with 1 terminal and 3 pairs posterolateral telson spines were grouped together, the range in size within the stage would become uncomfortably large, more than twice that of furcilia III and almost twice that in furcilia V. Variability in reduction of posterolateral spines was seen in furcilia VI and rarely in juvenile I.

The number of telson spines did relate to variation in size within a stage. For instance, furcilia III larvae that would molt from 7 to 3 terminal spines were 0.04 mm smaller on the average than those that would molt from 7 to 1 terminal spine and in furcilia IV, larvae with 3 terminal spines were 0.08 mm smaller on the average than those with 1 terminal spine. Variation in morphology within a stage was assessed in a sample of larvae from one location, as by midfurcilia phase there was a noticeable difference in rate of development between areas within the range of the population. It may be seen, for example, in a comparison of the length of larval stages at two locations in the California Current terminus (Figure 11) that, although they were smaller on the average, furcilia VI larvae from Station 10 in the mouth of the Gulf of California were within the size range of juvenile I of the slower growing larvae from Station 6 off western Baja California. The patterns of telson spine reduction in furcilia III-VI and juvenile I at these two locations, shown in Table 7, exemplify variation within the stages which appears to reflect the difference in rate of growth and morphogenesis.

South Pacific Population

Larvae from two areas within the southern range of *E. eximia* (Figure 1) were compared with larvae from the California Current terminus and, although the populations were generally similar, discrepancies were discovered. The most conspicuous differences proved to be in the armature of the telson. Among larvae in the South Equatorial and Peru Current population (southern form), the middle posterolateral spine was longer relative to the other two posterolateral spines and the majority of larvae had one pair of lateral spines only in all stages (Figure 12, Table 8); northern form larvae had 2 pairs of lateral telson spines from furcilia V. Furcilia III was slightly more variable in number of terminal telson spines while furcilia IV was less variable (Table 1). The carapace differed also with relatively longer posterodorsal spines from calyptopis I to furcilia I (Figures 3e-g, 8e) and sometimes with slightly larger and more persistant marginal spines.

Development of appendages was usually similar in the two forms. The lateral spine of the antennule was sometimes shorter and the lappet less developed in southern form furcilia VI and the setation of maxillule basal endite differed: 20, 62, and 75% of larvae examined had acquired 2 setae on the proximal margin of endite in furcilia V, VI, and juvenile I among northern form larvae while only 0, 2, and 17% of southern form larvae had a second seta in these stages.

Southern form larvae were smaller on the average in the furcilia phase but, as in the California Current terminus, differences in growth per stage between areas within the range of the population were noted. Developmental stages of *E. eximia* from the Peru Current (Stations 1520/1604) were larger on the average than those from the South

TABLE 7.—Pattern of telson spine reduction in furcilia III-VI and juvenile I in the northern form of *Euphausia eximia* at two locations (Stations 6 and 10) in the California Current terminus. Values indicate percentage with telson armature in stage.

		Terminal + posterolateral telson spines								
Stage	Stn	7+3	6+3	5+3	4+3	3+3	2+3	1+3	1+2	*n*
Furcilia III	6	100.0	—	—	—	—	—	—	—	280
	10	97.0	—	1.5	—	1.5	—	—	—	68
Furcilia IV	6	—	0.7	2.9	5.1	36.7	21.1	33.5	—	275
	10	—	—	—	—	15.1	19.0	65.9	—	126
Furcilia V	6	—	—	—	—	—	—	100.0	—	41
	10	—	—	—	—	—	—	100.0	—	97
Furcilia VI	6	—	—	—	—	—	—	92.9	7.1	14
	10	—	—	—	—	—	—	21.4	78.6	14
Juvenile I	6	—	—	—	—	—	—	25.0	75.0	12
	10	—	—	—	—	—	—	—	100.0	24

TABLE 8.—Number of pairs of lateral telson spines in furcilia IV-VI, juvenile I, and adult in northern and southern forms of *Euphausia eximia*. Values indicate percentage with telson armature in stage.

		Pairs of lateral telson spines				
Stage	Form	1	2	3	4	*n*
Furcilia IV	Northern	51.7	48.3	—	—	87
	Southern	98.4	1.6	—	—	61
Furcilia V	Northern	2.8	97.2	—	—	71
	Southern	97.9	2.1	—	—	48
Furcilia VI	Northern	5.8	94.2	—	—	52
	Southern	100.0	—	—	—	67
Juvenile I	Northern	1.8	98.2	—	—	55
	Southern	95.0	5.0	—	—	60
Adult	Northern	5.6	85.7	7.9	0.8	126
	Southern	97.5	2.5	—	—	121

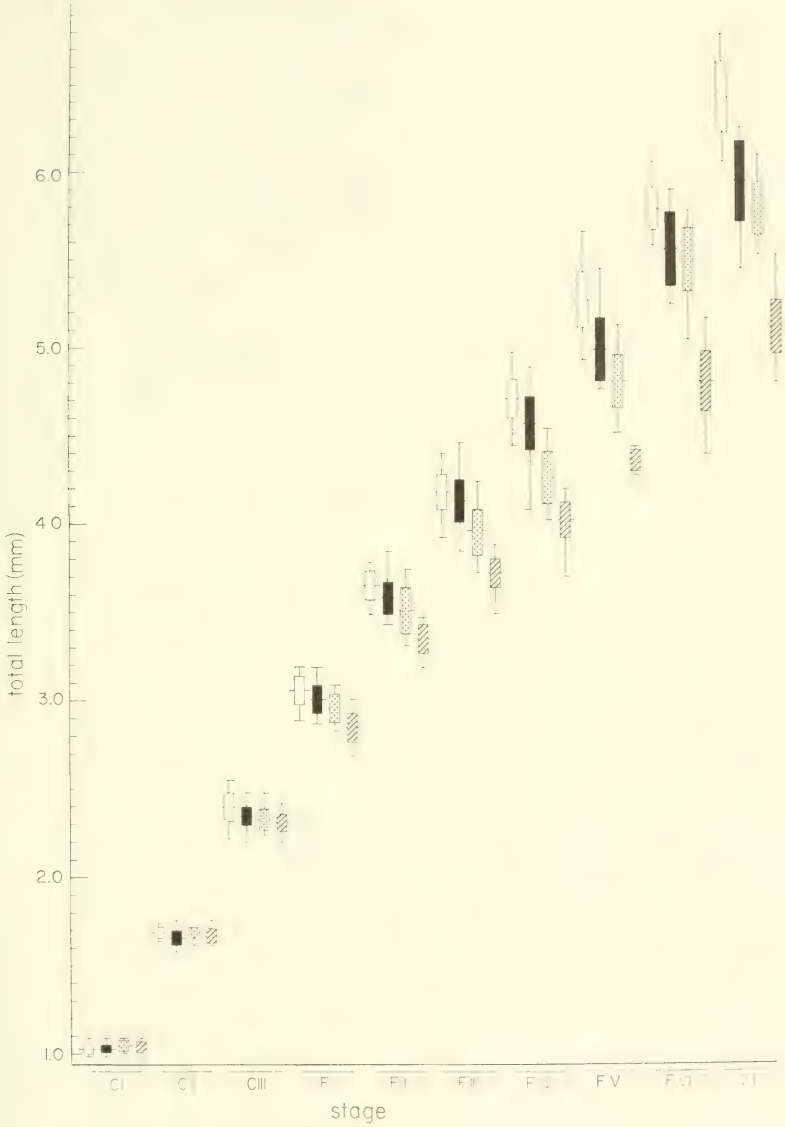


FIGURE 11.—Length of developmental stages of northern and southern forms of *Euphausia eximia* at four locations: mouth of Gulf of California, Station 10 (white); west of Baja California, Station 6 (black); Peru Current, Stations 1520 1604 (dots); South Equatorial Current, Station 21 (diagonal lines); vertical lines indicate range, horizontal lines indicate mean, and rectangles indicate sample standard deviations.

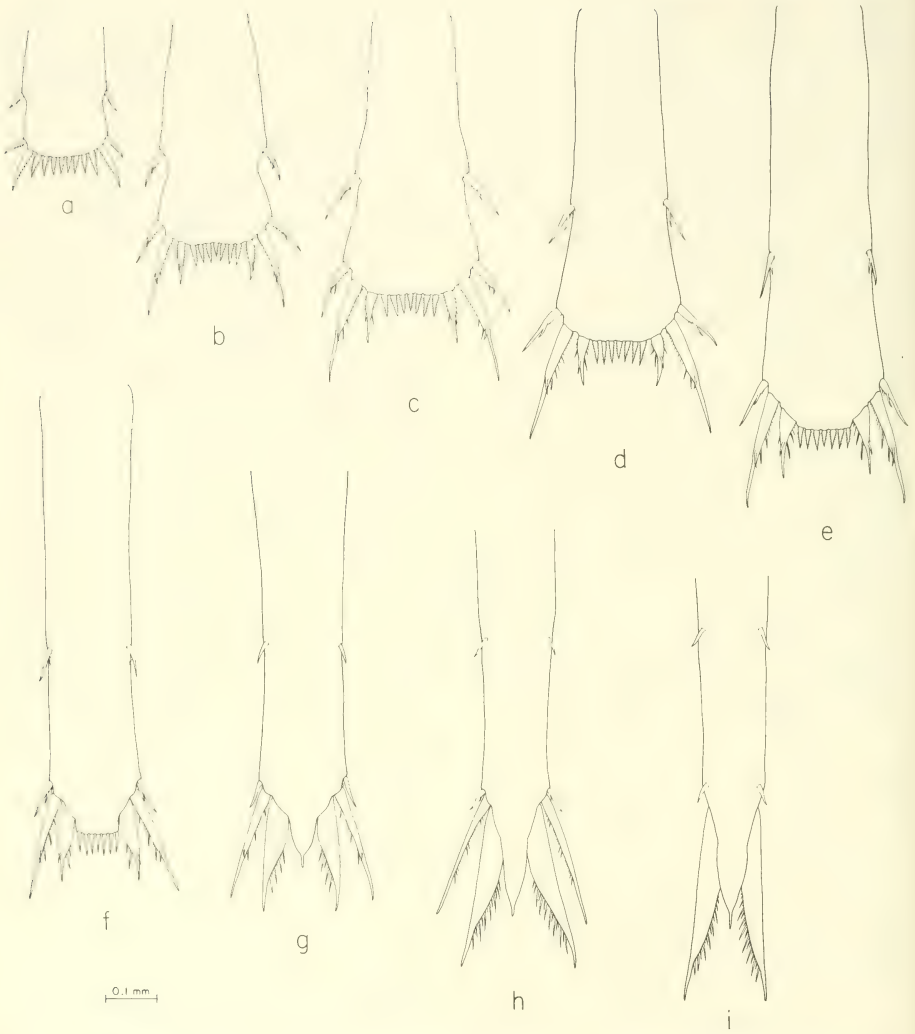


FIGURE 12.—*Euphausia eximia*, southern form. Telson, dorsal view: a-c, calyptopis I-III; d-i, furcilia I-VI.

Equatorial Current (Station 21). The lengths of larvae from these two locations are compared in Figure 11 (there were few furcilia V at Station 21 and consequently a small range in total length of this stage). Proportions of carapace length and telson width to total length were, on the average, as in northern form larval stages.

Because of the differences encountered between northern and southern form larvae, a preliminary survey of a few adult morphological characters

was carried out on samples of *E. eximia* from across the species' range. Variation in number of pairs of lateral telson spines was found to persist in the adult (Table 8) and a discrepancy in the armature of antennular peduncle, described and photographed by Roger (1967) in equatorial *E. eximia*, was found as well. The inner process of antennular peduncle segment 2 had 1 or 2 spines in the northern form and 1-5 spines in southern form adults (Table 9) and the number of spines was related to size. Northern form adults <21 mm TL had 1 spine only; 1 or 2 spines were found only on the largest animals of 21-27 mm. Southern form *E. eximia* of 12-18 mm length had 1-4 spines but animals >18 mm had 2-5 spines; 1 spine was not seen on the larger adults. Armature of the process was often asymmetrical.

The differences between populations of *E. eximia* in frequency of numbers of lateral spine pairs on the telson of furcilia V-VI and adult, and in armature of adult antennular peduncle segment 2 proved highly significant ($P = <0.005$) in chi-square analyses.

TABLE 9.—Number of spines on inner process of antennular peduncle segment 2 in adults of the northern and southern forms of *Euphausia eximia*. Values indicate percentage with armature in form.

	Number of spines on inner process, antennular peduncle segment 2					
Form	1	2	3	4	5	Number
Northern	93.2	6.8	—	—	—	117
Southern	21.2	33.9	33.1	11.0	0.8	118

Vertical Distribution

When larvae were sorted for taxonomic study, they were also counted at three stations in day and night series of vertical samples taken during Krill Expedition (Brinton 1979). The data obtained are presented in Tables 10-12.

At Station 6, west of Baja California in the California Current (Table 10), the distribution of eggs corresponded with the nighttime range of adults indicating that the majority of female *E. eximia* had spawned in the surface waters during the night. The highest concentration of metanauplii was found in the layer below the surface, reflecting sinking of eggs prior to hatching (Mauchline and Fisher (1969) note that eggs of *Thysanoessa raschii* and *Meganyctiphanes norvegica* sank at 5.5-7.5 m/h in water of 33.3‰ and 15° C). The majority of calyptopes and early furcilia stages were in the surface layer during the day, sinking to strata beneath at night. The pattern shifted gradually in midfurcilia phase and from furcilia III, the stage when all pleopods are setose, the larvae moved deeper in the daytime and toward the surface at night, and developed stronger migrating capability with increasing size.

The larval population structure and distribution pattern varied at Station 10 in the mouth of the Gulf of California (Table 11). No eggs were found and larvae were most abundant in early furcilia stages instead of in the metanauplius and calyptopis phases. The metanauplii were seen at the surface, and there was no evidence of nightly

TABLE 10.—Vertical distribution (percentage of stage at depth) of larvae and adults of *Euphausia eximia* in day and night samples from the California Current terminus off western Baja California (Station 6) and number/1,000 m³ in each stage.

			Calyptopis			Furcilia						
Depth (m)	Eggs	Metanauplius	I	II	III	I	II	III	IV	V	VI	Adult
Day:												
0-43	97.2	26.2	99.6	99.9	100.0	99.3	95.0	67.7	51.4	40.5	—	—
43-86	2.4	73.6	0.3	—	—	—	5.0	16.5	18.0	33.1	60.0	—
86-129	—	0.1	—	—	—	—	—	12.8	14.9	13.5	—	—
129-172	—	—	—	—	—	—	—	3.0	15.7	10.8	40.0	—
182-275	0.3	(<0.1)	0.1	0.1	—	—	—	—	—	—	—	100.0
275-368	0.1	0.2	—	—	—	—	—	—	—	—	—	—
368-461	—	—	(<0.1)	0.1	—	0.7	—	—	—	—	—	—
461-554	—	—	—	—	—	—	—	—	—	—	—	—
No./1,000 m³	3,283	10,593	7,510	3,835	991	288	100	436	255	37	5	28
Night:												
0-43	88.1	5.7	1.3	1.5	3.8	0.7	0.8	11.1	48.8	50.0	77.8	69.1
43-86	8.4	79.5	70.7	54.5	41.1	52.9	70.7	74.4	51.2	50.0	22.2	15.6
86-129	3.5	14.8	28.0	44.0	55.0	46.4	28.4	14.5	—	—	—	15.3
129-172	—	—	—	—	0.1	0.1	0.1	—	—	—	—	—
182-275	—	—	—	—	—	—	—	—	—	—	—	-
275-368	—	—	—	—	—	—	—	—	—	—	—	—
368-461	—	—	—	—	—	—	—	—	—	—	—	—
461-554	—	—	—	—	—	—	—	—	—	—	—	—
No./1,000 m³	143	5,402	4,380	2,089	4,018	1,180	874	379	125	18	9	392

TABLE 11.—Vertical distribution (percentage of stage at depth) of larvae and adults of *Euphausia eximia* in day and night samples from the California Current terminus off the mouth of the Gulf of California (Station 10) and number/1,000 m³ in each stage.

			Calyptopis			Furcilia						
Depth (m)	Eggs	Metanauplius	I	II	III	I	II	III	IV	V	VI	Adult
Day:												
0-43	—	—	99.7	99.8	99.9	99.8	99.8	99.3	79.0	33.2	41.2	—
43-136	—	—	0.3	0.2	0.1	0.2	0.2	0.7	21.0	61.8	45.1	—
136-229	—	—	—	—	—	—	—	12.8	14.9	13.5	—	—
229-322	—	—	—	—	—	—	—	—	—	—	7.8	—
322-415	—	—	—	—	—	—	—	—	—	—	—	100.0
No./1,000 m³	—	—	1,021	2,083	3,439	5,522	5,567	1,751	376	382	51	72
Night:												
0-43	—	100.0	100.0	100.0	100.0	99.9	99.8	96.9	93.3	100.0	100.0	72.2
43-86	—	—	—	—	—	0.1	0.2	3.1	6.7	—	—	27.8
86-129	—	—	—	—	—	—	—	—	—	—	—	—
129-222	—	—	—	—	—	—	—	—	—	—	—	—
222-315	—	—	—	—	—	—	—	—	—	—	—	—
315-408	—	—	—	—	—	—	—	—	—	—	—	—
408-501	—	—	—	—	—	—	—	—	—	—	—	—
No./1,000 m³	—	249	79	1,223	3,464	4,260	4,508	1,651	416	150	11	126

TABLE 12.—Vertical distribution (percentage of stage at depth) of larvae and adults of *Euphausia eximia* in day and night samples from the South Equatorial Current (Station 21) and number/1,000 m³ in each stage.

			Calyptopis			Furcilia						
Depth (m)	Eggs	Metanauplius	I	II	III	I	II	III	IV	V	VI	Adult
Day:												
0-37	10.2	—	73.4	58.5	48.1	30.3	11.1	14.1	13.1	28.1	—	—
37-75	41.2	20.6	14.7	31.8	36.9	48.6	56.2	45.7	34.0	—	—	—
75-112	27.5	58.8	—	0.4	—	0.8	7.0	10.5	20.0	—	13.6	—
112-150	20.8	20.1	11.9	9.3	14.7	20.3	25.7	29.7	31.9	34.4	9.1	—
150-227	0.1	0.3	—	—	—	—	—	—	—	—	—	—
227-305	0.2	0.2	—	—	0.3	—	—	—	0.9	37.5	77.3	36.1
305-382	0.1	—	—	—	—	—	—	—	—	—	—	63.9
382-460	—	—	—	—	—	—	—	—	—	—	—	—
No./1,000 m³	35,600	2,184	1,734	2,144	1,285	650	844	1,330	429	32	66	391
Night:												
0-36	21.7	—	25.7	31.9	34.5	35.4	20.4	6.4	16.8	—	19.9	45.1
36-72	20.1	—	59.3	62.1	60.1	51.0	49.1	49.1	50.4	100.0	80.1	39.8
72-108	56.2	98.0	14.1	5.9	5.3	13.3	30.5	43.9	32.8	—	—	15.1
108-144	0.5	—	—	—	—	0.3	—	—	—	—	—	—
144-223	1.4	2.0	0.8	0.1	—	—	—	—	—	—	—	—
223-302	(< 0.1)	—	—	—	—	—	—	—	—	—	—	—
302-381	(< 0.1)	—	—	—	—	—	—	—	—	—	—	—
381-460	—	—	—	—	—	—	—	—	—	—	—	—
No./1,000 m³	4,478	653	1,605	2,784	2,331	933	407	328	125	25	312	11,388

sinking of calyptopes and early furcilia larvae; almost the entire population remained in the surface layer until furcilia III. Diurnal vertical migration again developed in the last half of the furcilia phase.

The pattern of vertical distribution at Station 21 in the South Equatorial Current (Table 12) had features in common with the distribution observed at Station 6 but was less clearly defined. The position of the calyptopes reflected a developmental ascent from the depth at which eggs had hatched; calyptopis I was more abundant in the surface layer during the day than at night, and there was also some evidence of nighttime sinking in calyptopis II and III. In the furcilia phase the pattern of vertical migration was modified in that the larvae appeared to avoid the surface 0-35 m stratum to some extent. The population structure differed with calyptopis II being the most abundant larval stage.

The differences in larval vertical distribution appeared not to be related to time of sampling; in the upper 150-200 m, where most of the larvae were found, the three night samples were taken between 0000 and 0030 and the day samples in midafternoon (1600) at Stations 6 and 21 and midmorning (0800-0900) at Station 10 (Brinton 1979, figure 3).

DISCUSSION

The species of *Euphausia* were separated into groups, characterized by adult armature of carapace, abdomen, antennule, and petasma, by

Brinton (1975). Among species which have two lateral denticles on the carapace (group IA), *E. eximia* is most closely related to *E. krohnii* and *E. americana* by the conspicuous pectinate dorsal lappet on the first segment of the antennular peduncle. The larvae of *E. krohnii* have been described from the North Atlantic and Mediterranean by Frost (1934) and Casanova (1974) and, while it is not possible to compare the species in detail, the development of *E. eximia* appears to be very similar to that of the North Atlantic population of *E. krohnii*. The timing of acquisition of pigmentation in abdominal photophores may differ; Frost notes that all are pigmented in furcilia III but this condition was not normally seen in *E. eximia* until furcilia V. Development of the distinctive antennular lappet appears to begin at about the same stage (in furcilia V of *E. eximia* at 4.5-5.7 mm TL and in 5.9-6.1 mm larvae of North Atlantic *E. krohnii*) and with variable form. According to Soulier (1963) the lappet of Mediterranean *E. krohnii* develops in a fixed pattern, and >2 spines are not seen until 10 mm TL. There was greater variability in number of telson spines in furcilia IV of *E. eximia*, and one more stage in the furcilia phase, than noted by Casanova (1974) in *E. krohnii* from the Mediterranean. Larvae of the California Current population of *E. eximia* were intermediate in size between the large North Atlantic larvae of *E. krohnii* and the smaller Mediterranean population, while larvae of *E. eximia* from the South Equatorial Current tended to be similar in overall length to Mediterranean *E. krohnii*.

Larval forms appear to be very similar within *Euphausia* species group IA which, besides *E. eximia*, *E. krohnii*, and *E. americana*, includes *E. recurva*, *E. mutica*, *E. brevis*, and *E. diomedeae*. Their larvae share the following characters: spines on anterior margin of carapace in metanauplius, calyptopis phase, and early furcilia stages; a posterodorsal spine on carapace in calyptopis I-III and furcilia I; telson with middle posterolateral spine relatively long until midfurcilia phase; and a fixed pattern of pleopod development which progresses from 1 pair nonsetose to 1 pair setose plus 4 pair nonsetose, and finally to 5 pairs setose pleopods. Talbot (1974) noted variation in number of telson spines developing beneath the cuticle of furcilia III in *E. recurva-mutica* of the Agulhas Current, and Casanova (1974) described timing of events among larvae of *E. brevis* (e.g., modification of antenna and mandible, and development of legs), which is similar to the pattern discerned in *E. eximia*.

Developmental events may vary considerably, however, between the species groups of *Euphausia*. *Euphausia eximia* (group IA) and *E. gibboides* (group IB) differ in several details, some of which are listed in Table 13, although they share all the general features of group IA larvae except pattern of pleopod development. Larvae of *E. gibboides* are larger than those of *E. eximia*, on the average, in the metanauplius and calyptopis phases but they are similar in the furcilia phase due to a slightly higher rate of growth per stage in furciliae of *E. eximia*. The telson is wider in *E. gibboides* from calyptopis I through furcilia I, and the carapace is wider from calyptopis I-III, than in *E. eximia*, with no overlap in range of measurements.

The morphological differences observed within *E. eximia*, between larvae from the California Current terminus and the South Equatorial-Peru Current populations, appear related to the geographical separation of reproductive centers described by Brinton (1979) in his study of the distributional adaptations of euphausiids to the oxygen-deficient eastern tropical Pacific. He found that *E. eximia* achieved the highest densities (>500 beneath 1 m²) in the South Equatorial Current and across the California Current-eastern tropical Pacific transition off Baja California, the productive zones marginal to the low oxygen waters. The species occurred consistently across a transect of the eastern tropical Pacific but only

TABLE 13.—Some differences in larval development of *Euphausia eximia* and *E. gibboides*.

Feature	*E. eximia*	*E. gibboides*
Pleopods: pattern of development from furcilia I (' = nonsetose, " = setose)	1 → 1 4' → 5"	1 → 1 3 → 4 1 → 5
Telson: dominant pattern of terminal spine reduction from furcilia III to VI	7 → 3/1 → 1 → 1	7 → 5 → 3 → 1
innermost posterolateral spine, inner margin	With spinules	With distal spinule only from furcilia III
number of lateral spines	2 pairs from furcilia V	1 pair
Carapace: stage when anterior median spine develops	Furcilia I	Furcilia V-VI
Antennule: stage when dorsal lappet develops	Furcilia V-VI	Juvenile
Antenna: stage when modified to juvenile form	Furcilia IV	Furcilia V
Mandible: stage when modified to juvenile form	Furcilia IV	Furcilia VI
lateral knob in calyptopis phase	Absent	Present

sparsely (<4 under 1 m^2) from lat. 11° to 20° N where the surface temperature exceeded 26° C and lowest middepth O_2 values were <0.05 ml/l through a stratum of 600 m, and where water of westerly origin entered with the Equatorial Countercurrent. Larvae were not observed between lat. 2° and 20° N.

The significant difference in frequency of numbers of lateral telson spines on late furciliae of the California Current and the South Equatorial and Peru Currents may be evidence of the development of reproductive isolation between the two populations. The larval evidence was corroborated by a preliminary survey of adult *E. eximia* which showed a significant difference between populations in the armature of both telson and antennular peduncle. A more thorough examination of adult morphology is necessary, however, for an evaluation of the divergence within the species. The distribution of northern and southern forms observed (Figure 1) suggests that juveniles and adults of *E. eximia* are carried from the species' reproductive center off Baja California into the oxygen-deficient warm waters of the eastern tropical Pacific which may form an effective barrier between the reproductive areas of the two populations.

Variation in size of larvae at the same stage of development (Figure 11) between areas sampled within each population may be related to the amount of food available among other factors. Le Roux (1974), investigating the effects of diet and temperature on the larval development of *Meganyctiphanes norvegica*, demonstrated that rhythm of molt, growth, and morphogenesis were influenced by quality and quantity of food. With excess food, an elevation in temperature caused an acceleration in rate of molt but not precocious differentiation and reduction of the number of larval stages; the larvae were found to be a little smaller in a given stage at the higher temperature due to a decrease in growth per molt.

The relationship of surface temperature to size among *E. eximia* larvae studied was not consistent. Relatively smaller larvae were found at the higher temperature within the South Equatorial-Peru Current population (22° and 16° C at Stations 21 and 1520/1604) but in cooler waters of the California Current (18° and 24° C at Stations 6 and 10). There was a direct correlation of size with abundance of food, however, among California Current larvae; the volume of zooplankton biomass was very low at Station 6 but relatively high at Station 10 (Brinton 1979) reflecting displacement upward of recently upwelled waters with high concentrations of nutrients and probably, with relatively green waters, abundant food for larval forms. The larger size of larvae from Station 10 may also be related to their position in the water column; numbers of calyptopes and early furcilia at Station 6 sank below the surface stratum at night while those at Station 10 remained almost entirely day and night in the food-rich surface layer. Data on biomass and on larval vertical distribution were not available for Stations in the Peru Current for comparison with those in the South Equatorial Current.

Most species of euphausiids studied show indications of some downward daytime vertical migration from calyptopis II (Mauchline and Fisher 1969) but at Stations 6 and 21 (Tables 9, 11) the position of *E. eximia* calyptopes in day and night samples appeared to indicate a reverse pattern of movement. After a presumed developmental ascent from the depths at which nauplii hatched from sinking eggs, the majority of calyptopis I were found in the surface layer in the daytime and in deeper strata at night. The pattern continued through furcilia III at Station 6 and through calyptopis III, to some extent, at Station 21. As noted above, most larvae at Station 10 were found in the surface stratum in both day and night samples through furcilia II; the lack of nighttime sinking in early stages may be related to the shoaling of low oxygen water and upwelling conditions observed in the area (Brinton 1979).

The position of calyptopis I in the day-night series at Stations 6 and 21 suggests that the larvae were drawn to the surface layer by positive phototaxis. Sulkin (1973), working with two species of xanthid brachyurans, showed that, in the absence of light, the distribution of larvae varied with ontogeny; the four zoeal and one megalopa stage assumed a differential vertical distribution due to forces of gravity and hydrostatic pressure as well as different sinking rates, with early stages near the surface. In assessing the influence of light on depth regulation in the same species, Sulkin (1975) suggested that the observed positive phototaxis superimposed a diurnal vertical migration on the basic pattern of differential ontogenetic vertical distribution. Larvae of *E. eximia* appear to show a similar response during the calyptopis phase with modification of their behavior during ontogeny as furcilia develop a pattern of vertical migration similar to that of the adult.

ACKNOWLEDGMENTS

I thank E. Brinton for his advice and criticism of the manuscript, A. Fleminger for dissection of furcilia to confirm morphology of mandibles, and A. Townsend for helpful discussions of larval morphology. I am also grateful to the *Fishery Bulletin* reviewers for their constructive comments. This work was supported by the Marine Life Research Program, the Scripps Institution of Oceanography's component of the California Cooperative Oceanic Fisheries Investigations.

LITERATURE CITED

ANTEZANA-JEREZ, T.
1978. Distribution of euphausiids in the Chile-Peru Current with particular reference to the endemic *Euphausia mucronata* and the oxygen minima layer. Ph.D. Thesis, Univ. California, San Diego, 466 p.

BRINTON, E.
1962. The distribution of Pacific euphausiids. Bull. Scripps. Inst. Oceanogr., Univ. Calif. 8:51-269.
1967. Distributional atlas of Euphausiacea (Crustacea) in the California Current region, Part I. Calif. Coop. Oceanic Fish. Invest., Atlas 5, 275 p.
1975. Euphausiids of southeast Asian waters. Naga Rep. 4(5), 287 p.
1979. Parameters relating to the distributions of planktonic organisms, especially euphausiids in the eastern tropical Pacific. Prog. Oceanogr. 8:125-190.

CASANOVA, B.
1974. Les Euphausiacés de Mediterranée. (Systematique et développement larvaire. Biogéographie et biologie.) Doctoral Thesis, l'Université de Provence (Aix-Marseille I), 380 p.

FRASER, F. C.
1936. On the development and distribution of the young stages of krill (*Euphausia superba*). Discovery Rep. 14:1-192.

FROST, W. E.
1934. The occurrence and development of *Euphausia krohnii* off the southwest coast of Ireland. Proc. R. Ir. Acad., Sect. B, 42:17-40.

GOPALAKRISHNAN, K.
1973. Developmental and growth studies of the euphausiid *Nematoscelis difficilis* (Crustacea) based on rearing. Bull. Scripps Inst. Oceanogr., Univ. Calif. 20, 87 p.

GURNEY, R.
1942. Larvae of decapod crustacea. Ray Soc. Publ. 129, Ray Soc., Lond., 306 p.

KNIGHT, M. D.
1975. The larval development of Pacific *Euphausia gibboides* (Euphausiacea). Fish. Bull., U.S. 73:145-168.
1978. Larval development of *Euphausia fallax* Hansen (Crustacea: Euphausiacea) with a comparison of larval morphology within the *E. gibboides* species group. Bull. Mar. Sci. 28:255-281.

LASKER, R., AND G. H. THEILACKER.
1965. Maintenance of euphausiid shrimps in the laboratory. Limnol. Oceanogr. 10:287-288.

LE ROUX, A.
1974. Observations sur le développement larvaire de *Meganyctiphanes norvegica* (Crustacea: Euphausiacea) au laboratoire. Mar. Biol. (Berl.) 26:45-56.
1976. Observations sur les larves de *Nyctiphanes couchii* et de *Meganyctiphanes norvegica* (Crustacea: Euphausiacea) récoltées dans le Golfe du Morbihan. [Engl. summ.] Cah. Biol. Mar. 17:375-386.

MAUCHLINE, J., AND L. R. FISHER.
1969. The biology of euphausiids. Adv. Mar. Biol. 7, 454 p.

ROGER, C.
1967. Note on the distribution of *Euphausia eximia* and *E. gibboides* in the equatorial Pacific. Pac. Sci. 21:429-430.

SOULIER, B.
1963. Pêches planctoniques, superficielles et profondes, en Méditerranée Occidentale. IV. Euphausiacés. Rev. Trav. Inst. Pêches Marit. 27:417-440.

SULKIN, S. D.
1973. Depth regulation of crab larvae in the absence of light. J. Exp. Mar. Biol. Ecol. 13:73-82.
1975. The influence of light in the depth regulation of crab larvae. Biol. Bull. (Woods Hole) 148:333-343.

TALBOT, M. S.
1974. Distribution of euphausiid crustaceans from the Agulhas Current. Zool. Afr. 9:93-145.

WEIGMANN-HAASS, R.
1977. Die Calyptopis- und Furcilia-Stadien von *Euphausia hanseni* (Crustacea: Euphausiacea). Helgol. wiss. Meeresunters. 29:315-327.

FEEDING ECOLOGY OF *LAGODON RHOMBOIDES* (PISCES: SPARIDAE): VARIATION AND FUNCTIONAL RESPONSES

ALLAN W. STONER[1]

ABSTRACT

Five major ontogenetic stages were found in the diet of pinfish, *Lagodon rhomboides*, from Apalachee Bay, Florida, but diet and dietary breadth showed high degrees of variation with space (both local and geographic), and seasonal variation within size classes was often as dramatic as ontogenetic variation. *Lagodon rhomboides* demonstrated planktivory, omnivory, strict carnivory, and strict herbivory at different times, places, and developmental stages.

Ontogenetic pattern in food habits was primarily a function of mouth size and changing dentition of the predator. Until it reaches 35 mm standard length, the pinfish is an obligate carnivore. Spatial and temporal variation in the food habits of pinfish was a complex function of absolute and relative abundances of food items in the field. Changes in plant consumption by fish larger than 35 mm standard length may be due to changing plant abundance or protection of prey species by macrophyte cover at a given station. Since seagrass biomass and the functional role of a single predator vary over both space and time, plant-animal and predator-prey relationships change continually; however, the life history of *L. rhomboides* is well adapted to seasonal patterns of productivity in food organisms. Multidimensional variation in diets rendered the trophic level concept inoperational. It is concluded that food webs are static neither in time nor in space and that taxonomic species may not be functional components in models of energetic pathways and predator-prey relationships.

In recent years, much research effort has been expended on experiments for testing the role of predation in seagrass meadows (Young et al. 1976; Young and Young 1977, 1978; Orth 1977; Nelson 1978; Reise 1978); yet few experimental ecologists have concerned themselves with variation in the feeding behavior or functional responses of the predators involved in their experiments. The problem is illustrated by empirical data which show the potential for wide variation in the diets of fishes with season (Keast and Welsh 1968; Bell et al. 1978a, b), time of day (Hobson 1974; Hobson and Chess 1976; Robertson and Howard 1978), age or size of the animal (Carr and Adams 1973; Hobson and Chess 1976; Ross 1978), and with locality (Feller and Kaczynski 1975; Love and Ebeling 1978). However, very few scientists have adequately characterized interactions of spatial, temporal, and ontogenetic variations (Keast 1970, 1979; Nakashima and Leggett 1975). Also, field studies that have examined relationships between prey selection by fish and structure of prey assemblages are largely limited to fishes that inhabit structurally simple mud bottom or water column habitats (Feller and Kaczynski 1975; Nakashima and Leggett 1975; Repsys et al. 1976; Stein 1977). To date, only two field studies provide data on the functional responses of fish to prey abundance in seagrass habitats. Robertson and Howard (1978) reported that short-term (diel) dietary shifts in fishes inhabiting beds of *Zostera muelleri* and *Heterozostera tasmanica* were due to vertical movements of holoplankton and facultative zooplankton. Stoner (1979b) showed that the selectivity of prey by pinfish, *Lagodon rhomboides*, was mediated by standing crop of benthic macrophytes. I concluded that increased seagrass biomass resulted in a higher degree of selectivity for certain amphipod species by juvenile fish.

The pinfish is the numerically dominant fish on *Thalassia testudinum* meadows in the shallow subtidal areas of the Gulf of Mexico (Hoese and Jones 1963; Hansen 1969) and on *Z. marina* beds along the Atlantic coast of the United States south of Cape Hatteras, N.C. (Adams 1976). The pinfish is one of the most important predators on macrobenthic organisms of seagrass meadows and has been shown to play a role in the organization of faunal assemblages (Young et al. 1976; Young and Young 1978; Nelson 1978). Data have accumulated on the food habits of pinfish; however, most of the early work reviewed by Caldwell (1957) and

[1]Department of Biological Science, Florida State University, Tallahassee, Fla.; present address: Harbor Branch Institution, Inc., R.R. 1, Box 196-A, Fort Pierce, FL 33450.

Manuscript accepted December 1979.
FISHERY BULLETIN: VOL. 78, NO. 2, 1980.

Carr and Adams (1973) is qualitative and based on small numbers of fish with no particular attention paid to time, space, or fish size. Carr and Adams provided the best published account of food habits of pinfish, noting distinct ontogenetic patterns in the food habits of pinfish and several other fish species which dwell on seagrass beds near Crystal River, Fla. The general conclusion has been that *L. rhomboides* is a generalist feeder. Because *L. rhomboides* is an important mediator of benthic organization, and because the fish is a generalist-type feeder, an investigation was undertaken to test for functional responses of the species to food abundance in the field. Ontogenetic, spatial (local and geographic), and temporal (seasonal) variations in food habits of *L. rhomboides* were explained on the basis of predator morphology, food abundance, and habitat complexity.

METHODS

Based on long-term macrophyte data for the area (Zimmerman and Livingston 1976a, b), four collecting stations were chosen from shallow regions offshore from the mouths of the Econfina and Fenholloway Rivers, in Apalachee Bay, Fla. (Figure 1). One station was located 2.0 km seaward from each of the river mouths and a second was located 4.0 km seaward. Each site was identified with a permanent marker in a location which was representative of a broad area. Stations Econfina 10 and 12 were macrophyte-dominated habitats (primarily *T. testudinum* and *Syringodium filiforme*) with mean annual macrophyte biomasses of 214 and 320 g dry wt/m^2. The inner station of the Fenholloway area (station 11) was characterized by low macrophyte densities (9.3 g dry wt/m^2) and the outer station (Fenholloway 12) was characterized by macrophyte levels (141 g dry wt/m^2) intermediate between those levels found at the Econfina stations and those at the inner Fenholloway station (Livingston[2]). All stations were polyhaline with salinities ranging from approximately 17 to 34‰. The mean water depth at all stations was between 1.6 and 2.0 m.

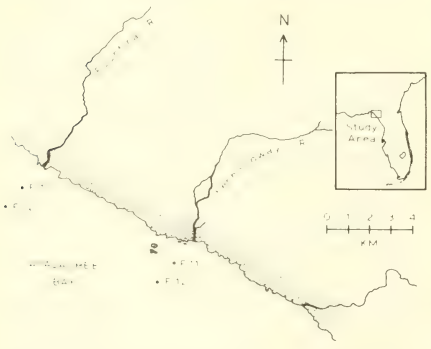


FIGURE 1.—Locations of collecting sites for *Lagodon rhomboides* and food organisms offshore from the Econfina and Fenholloway Rivers in Apalachee Bay, Fla.

Pinfish were collected with a 5 m otter trawl (1.9 cm mesh wing and body, 0.6 cm mesh liner). Seven 2-min tows (2-3 kn) were taken at each station on a monthly basis. The trawling method for the study site was examined by Livingston et al.[3] All tows were made at midday since previous work (Kjelson et al. 1975; Peters and Kjelson, 1975; Adams, 1976) indicated that pinfish feed primarily during daylight hours. All fishes were preserved in 10% Formalin[4]-seawater solution, identified to species, and measured for standard length (SL).

To estimate abundance of prey items in the field, macrobenthic animals (>0.5 mm) and zooplankton were collected on each of the fish collection dates. Macrobenthic prey items were collected with 12 7.6 cm diameter cores and identified to species (Stoner in press). Zooplankton were collected with horizontal tows of a 0.5 m simple conical plankton net with 0.202 mm mesh and a T.S.K. flowmeter. A single tow was made at each station, on each sampling date, at a speed of 1.5 kn. Tow time was dependent upon the abundance of plankton but ranged from 2 to 10 min. Each plankton sample was subsampled with a Folsom plankton splitter when necessary and a 5 ml Hensen-Stemple pipette. One one-hundredth of each sample was counted. Since the importance of planktonic prey items in pinfish food habits was limited to a small part of the population, animals were identified only to major taxonomic group (e.g., calanoid copepod, crab zoea, polychaete larva, etc.)

[2]R. J. Livingston, Associate Professor, Department of Biological Science, Florida State University, Tallahassee, FL 32306, pers. commun. January 1978.

[3]Livingston, R. J., K. L. Heck, Jr., and T. A. Hooks. 1972. The ecological impact of pulp will effluent on aquatic flora and fauna of north Florida: Comparison of a polluted drainage system (Fenholloway) with an unpolluted one (Econfina). Unpubl. Rep., 186 p., to the Coastal Coordinating Council, Florida.

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

and the standing crops of each group were calculated.

Plants were quantitatively sampled (Livingston et al. 1976) at the field quadrant from where macrobenthic animals were collected, on the fish collection date. Data on the biomass and species composition of benthic macrophytes at the field stations were provided by Robert J. Livingston.

Fish, macrophytes, and prey animals were collected monthly from November 1976 to December 1977. All collections for a station were made on the same date at midday, and all of the stations were sampled within a 2-4 day period.

For analysis of stomach contents, fish were placed in 5 mm size classes up to 40 mm SL, 10 mm size classes from 40 to 100 mm, and 20 mm size classes for fish >100 mm SL. Food items taken from the stomachs of up to 25 fish in a size class were pooled for each sampling date and station and preserved with 70% isopropanol and a dilute solution of rose bengal stain. The gravimetric sieve fractionation procedure developed by Carr and Adams (1972) was used to analyze stomach contents of pinfish ranging from 11 to 160 mm SL. Stomach contents were washed through a series of six sieves of decreasing mesh size (2.0-0.075 mm mesh) and the frequency of occurrence of each food type was recorded for each sieve fraction. Because all of the items in a particular sieve fraction were of comparable size, the relative proportion of the stomach contents made up of each food type was measured directly by counting. After examination, each sieve fraction was dried overnight at 100° C and the total contribution of each food type was calculated.

With two exceptions, each food particle was placed in a mutually exclusive category. General categories such as amphipod, isopod, harpacticoid copepod, crab zoea, and mysid were employed. The categories animal remains (unidentified tissue stained with rose bengal) and plant remains were the only food categories that were not mutually exclusive from other groups. Plants specifically identified were *T. testudinum* and *S. filiforme*. The general food categories, 40 in number (Table 1), were used for statistical analyses; however, whenever an animal or plant could be identified to a more specific group (e.g., family, genus, species) this information was recorded.

Cluster analysis, employing the similarity coefficient, ρ (Matusita 1955; Van Belle and Ahmad 1974), and flexible grouping cluster strategy ($\beta = -0.25$) was used to describe ontogenetic variation in food habits of *L. rhomboides*. The appropriateness of the cluster strategy for dealing with fish diet data was discussed by Sheridan (1978).

TABLE 1.—List of the general food categories encountered in the stomachs of pinfish and the codes employed in food habit histograms.

Code	Food category	Code	Food category
AM	Amphipod	IS	Isopod
BA	Barnacle	IT	Invertebrate tube
BI	Bivalve	MY	Mysid
BR	Branchiuran	NE	Nematode
BZ	Bryozoan	NM	Nemertean
CC	Calanoid copepod	NU	Nudibranch
CH	Chaetognath	OS	Ostracod
CR	Crab	PL	Polychaete larvae
CU	Cumacean	PM	Plant matter
CZ	Crab zoea	PO	Polychaete
DE	Detritus	SA	Sand
DI	Diatom	SC	Scallop
FE	Fish egg	SH	Shrimp
FL	Fish larvae	SL	Spicule
FO	Foraminifera	SP	Shrimp postlarvae
FR	Fish remains	SY	*Syringodium filiforme*
GA	Gastropod	TA	Tanaid
HC	Harpacticoid copepod	TH	*Thalassia testudinum*
HY	Hydroid	VL	Veliger larvae
IE	Invertebrate egg		
MS	Miscellaneous — used in food habit histograms for all food items making up < 3% of the total mass.		

Stepwise multiple regression was used in certain instances to analyze the relationships between amounts of food items consumed by pinfish and abundance of food items in the field. Dependent variables included the amount of amphipod, shrimp, and plant material in stomachs (percent of contents in dry weight) and independent variables were amphipod, shrimp, plant, calanoid copepod, and polychaete abundance values. Maximization of the coefficient of determination, r^2, was the criterion for selecting the best multiple regression model. The minimum F value for inclusion of variables in the regression equations was set at 0.01.

RESULTS

Nearly 5,000 pinfish, representing 61% of all trawlable ichthyofauna in Apalachee Bay, were collected at four field sites during a 1-yr sampling period. The number of fish collected at a station, however, was a direct function of the mean macrophyte biomass at the site ($r = 0.998$, $P > 0.01$). Most of the fish were collected between April and October (Figure 2).

The stomach contents of 2,174 pinfish taken from the four field sites were analyzed. Although the unvegetated site (Fenholloway 11) produced only 82 pinfish in routine trawl collections, over 600 stomachs of fish from each of the vegetated

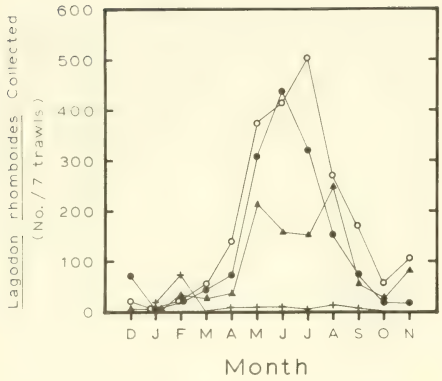


FIGURE 2.—Number of *Lagodon rhomboides* collected in Apalachee Bay, Fla., from December 1976 to November 1977. Crosses = Fenholloway 11, triangles = Fenholloway 12, dots = Econfina 10, circles = Econfina 12.

stations were examined. The relative proportions of various food items taken by pinfish of different size classes (for all dates and stations) varied widely with fish size (Figure 3) and cluster analysis showed four distinct ontogenetic trophic groups. The first group was planktivorous and includes only those fish <16 mm SL. The second group (16-35 mm) included fish which took harpacticoid copepods and amphipods in nearly equal proportions plus small amounts of shrimp postlarvae, invertebrate eggs, and other animals. This group was largely carnivorous. Fish of group three (36-80 mm) were omnivores, taking about 30% of their diet in the form of plant material (mostly microepiphytes) and the rest from the macrobenthic fauna (mainly amphipods, small shrimp, and some harpacticoid copepods). Group four (>80 mm) included mostly adult fish, >1 yr old. At least one-half of the diet was plant material; however, stomach contents of fish >100 mm SL were <10% animal matter. A large portion of the plant matter consumed was seagrass, especially *S. filiforme*.

Pinfish diet was dependent upon the place of capture as well as size of the fish (Table 2). Although a large percentage of the stomachs were empty, the primary food item of pinfish between 11 and 15 mm SL was calanoid copepods at Fenholloway 11, Fenholloway 12, and Econfina 12. Fish of the same size class took a large number of invertebrate eggs at the inner stations, Econfina 10 and Fenholloway 11. Harpacticoid copepods and

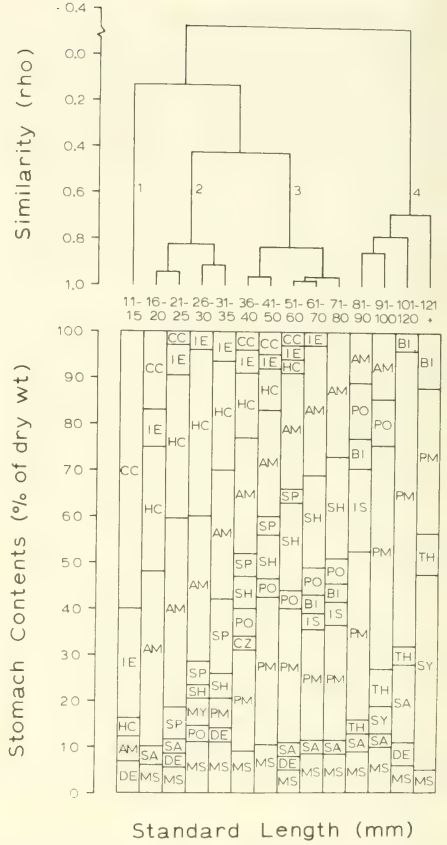


FIGURE 3.—Ontogenetic changes in diet of *Lagodon rhomboides* from Apalachee Bay, Fla. Histograms represent relative proportions of major dietary components (dry weight). Dendogram represents cluster analysis of diet similarity among size classes. Codes for the food items are given in Table 1. (See text for explanation of the cluster strategy.)

amphipods were important food items only at Econfina 10. The percentage of diet made up by calanoid copepods was directly related to the mean calanoid copepod standing crop (number per cubic meter) at a given station and time ($r = 0.804$, $P<0.05$) (Figure 4). No significant relationships were found between amphipods consumed by the small pinfish and abundance of amphipods in the field; however, amphipods were consumed by post-

TABLE 2.—Composition of stomach contents of *Lagodon rhomboides* at four stations in Apalachee Bay, Fla. Each value is the mean percentage of the total dry weight of stomach contents for the fish size class indicated.

Item	Fen 11	Fen 12	Econ 10	Econ 12
	SL = 11-15 mm			
n (% empty)	23(70.0)	10(70.0)	35(42.8)	28(42.8)
Calanoid copepods	58.1	91.9	17.3	79.7
Invertebrate eggs	23.9		47.7	8.8
Detritus	18.0	8.1		4.3
Harpacticoid copepods			19.0	2.3
Amphipods			16.0	4.9
	SL = 16-35 mm			
n (% empty)	14(14.3)	140(5.0)	213(1.4)	235(2.1)
Harpacticoid copepods	7.0	40.8	26.5	38.3
Amphipods	30.0	18.3	38.5	28.3
Invertebrate eggs	9.5	8.0	2.7	7.3
Shrimp postlarvae	3.0	6.0	13.5	7.5
Polychaetes		2.8	1.7	1.0
Plant matter		2.9	2.5	4.2
Shrimp	3.0	5.3	1.5	0.2
Calanoid copepods	40.0		1.0	5.2
Miscellaneous	7.5	15.9	12.1	8.0
	SL = 36-80 mm			
n (% empty)	35(8.6)	380(6.6)	460(3.0)	408(4.4)
Amphipods	56.8	27.2	27.2	30.1
Plant matter	16.5	25.3	30.0	23.0
Harpacticoid copepods	0.8	5.6	6.4	6.0
Shrimp postlarvae	0.8	2.8	4.2	1.4
Shrimp	1.3	12.3	9.7	17.7
Polychaetes	3.3	5.0	2.5	5.2
Calanoid copepods	3.3	2.9	2.6	3.6
Invertebrate eggs	0.8	3.5	2.9	5.0
Bivalves		3.7	0.4	
Miscellaneous	16.4	11.7	14.1	8.0
	SL > 80 mm			
n (% empty)	10(30.0)	85(15.3)	78(11.5)	20(15.0)
Plant matter	6.0	63.3	84.3	91.7
Polychaetes	0.7	4.9	0.1	
Amphipods	6.0	8.1	2.4	2.0
Bivalves	81.3	10.1	0.4	
Miscellaneous	6.0	13.6	12.8	6.3
Total number	82	615	786	691
% Empty	29.3	8.4	5.2	5.5

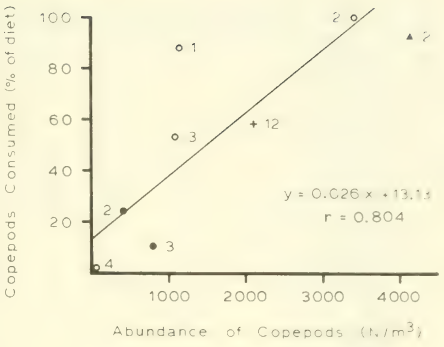


FIGURE 4.—Percentage of stomach contents (dry weight) of postlarval pinfish composed of calanoid copepods shown as a function of copepod abundance in Apalachee Bay, Fla. Cross = Fenholloway 11, triangle = Fenholloway 12, dots = Econfina 10, circles = Econfina 12. Months are indicated by numbers beside the plotted points.

larval fish at Econfina stations 10 and 12 only. The small epifaunal amphipod *Gitanopsis tortugae*, one of the few species consumed by small pinfish, was collected only at these two stations during these months (see Stoner (1979a) for a detailed analysis of prey species consumed by *L. rhomboides*). Because no data are available on abundance of harpacticoid copepods in Apalachee Bay, the importance of their abundance to food habits of pinfish remains unknown.

The main components of the diets of pinfish between 16 and 35 mm were amphipods, harpacticoid copepods, and shrimp postlarvae at the three vegetated sites; amphipods and calanoid copepods at Fenholloway 11. Shrimp and shrimp postlarvae were abundant at the vegetated stations, but few in number at the unvegetated site (Table 3). This probably explains the differences in shrimp consumption. Calanoid copepods were apparently substituted for shrimp at Fenholloway 11, although the copepods were less abundant at that site than at other stations (Econfina 10 and 12) between April and July (Table 3). Low abundance of harpacticoid copepods may explain their relatively low contribution to the food habits of young pinfish at the unvegetated site.

Diets of fish from 36 to 80 mm were similar at the three vegetated stations and included large amounts of amphipod, shrimp, and plant material. At the unvegetated site, amphipods made up approximately twice the percentage found in fish from vegetated stations. Because of low shrimp abundance at the unvegetated site, shrimp contributed little to the diets of fish inhabiting that site. Amphipods appear to have been substituted for shrimp.

Fish >80 mm demonstrated wide variability in the percentage of the stomach contents composed of plant material, ranging from 6.0% at Fenholloway 11 to 91.7% at Econfina 12. The diet of fish from the unvegetated station was dominated by the mussel *Brachidontes exustus*. For adult fish, the mean percentage of the diet composed of plant material was a direct function of the mean standing crop of benthic macrophytes at a given station ($r = 0.952$, $P<0.05$); however, there was wide temporal variation in the standing crop of benthic macrophytes at the vegetated sites (Table 3) which was not followed by proportional changes in plant consumption at Econfina 10 and Fenholloway 12.

TABLE 3.—Abundance of prey organisms and biomass of benthic macrophytes[1] in Apalachee Bay, Fla., from December 1976 to November 1977. Only epifaunal species commonly consumed by *Lagodon rhomboides* were included in the abundance of amphipods.

Stn	Prey organisms	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.
F 11	Amphipods, no./m²	95	0	38	189	114	0	152	0	0	95	152	151
	Shrimp, no./m²	19	0	0	0	0	19	19	38	38	0	19	0
	Polychaetes, no./m²	171	246	719	908	1,834	794	284	416	739	701	361	1,287
	Copepods, no./m³	2,144	4,423	3,469	946	659	0	327	2,232	4,651	2,583	1,576	1,775
	Macrophytes, g dry wt/m²	—	3	1	6	5	5	8	11	16	10	20	18
F 12	Amphipods, no./m²	379	246	152	245	1,209	397	479	246	454	794	730	1,493
	Shrimp, no./m²	57	38	38	0	94	38	190	19	341	133	76	57
	Polychaetes, no./m²	1,948	1,194	1,436	1,325	1,722	2,005	1,477	701	965	1,760	607	2,460
	Copepods, no./m³	1,973	5,935	4,182	2,202	81	109	411	798	2,730	3,123	1,792	686
	Macrophytes, g dry wt/m²	—	110	152	96	197	70	145	165	175	243	117	84
E 10	Amphipods, no./m²	114	76	359	870	1,133	2,910	1,514	416	1,720	567	302	1,846
	Shrimp, no./m²	19	0	19	19	19	0	95	189	114	114	208	208
	Polychaetes, no./m²	1,154	663	1,079	814	569	2,119	910	758	907	853	625	2,947
	Copepods, no./m³	1,020	543	385	803	1,981	7,130	1,069	4,042	3,404	2,898	1,315	1,227
	Macrophytes, g dry wt/m²	—	96	164	58	230	246	216	234	279	392	319	126
E 12	Amphipods, no./m²	926	1,191	2,230	1,190	813	1,512	1,000	624	339	435	549	1,343
	Shrimp, no./m²	76	19	19	38	76	0	57	57	95	38	76	0
	Polychaetes, no./m²	946	1,665	1,304	1,097	890	1,553	1,062	815	797	683	380	1,156
	Copepods, no./m³	807	1,147	3,440	1,070	0	527	258	1,387	3,447	2,745	2,136	948
	Macrophytes, g dry wt/m²	—	259	237	118	240	319	456	390	374	619	401	104

[1]Macrophyte data were provided by R. J. Livingston (see text footnote 2).

This point will be discussed later. Polychaetes, bivalves, amphipods, and other taxa were consumed by adult pinfish where macrophyte cover was low.

Seventy percent of the postlarval pinfish from Fenholloway stations were empty and 42.8% of the fish from Econfina stations had no stomach contents (Table 2). Empty stomachs in pinfish >15 mm SL were less common than found in postlarval fish, but fish collected at the unvegetated site consistently had the highest percentage of empty stomachs. Between 11.5 and 15.3% of adult fish taken from vegetated sites had empty stomachs, but 30% of the adults from Fenholloway 11 were empty.

Ontogenetic and spatial variations in pinfish diet were interrelated with changes in diet with season. Overall diet of the pinfish population at a given station was highly dependent upon the length-frequency composition of the population (Figure 5); therefore, to examine independently the effect of season on food habits, size was held constant. Individual size groups, based on the cluster analysis of feeding ontogeny (Figure 3) were tested for seasonality in diet. Although the mean length of fish in the 16-35 mm SL size class increased from 20 to 32 mm between March and August, an analysis of dietary changes within 5 and 10 mm size classes indicated that the bias was not serious and that the change in food habits over time within the larger size group was an accurate representation of dietary seasonality. Length-fre-

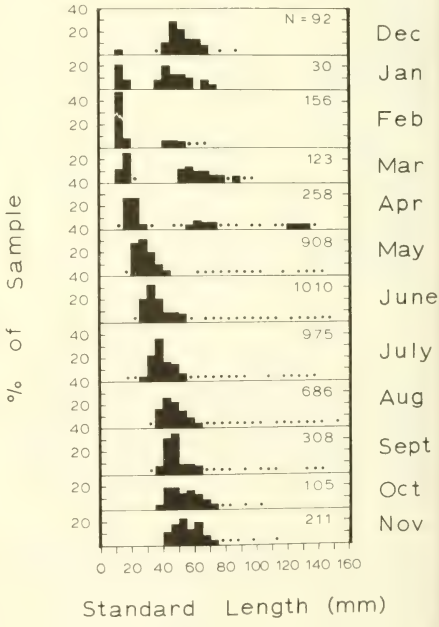


FIGURE 5.—Length-frequency distributions for *Lagodon rhomboides* collected in Apalachee Bay, Fla., from December 1976 to November 1977. Dots indicate that <3.0% of the sample occurred in the size class.

quency changes related to season within the 36-80 mm and adult size groups were minor. Because of insufficient data for the site, Fenholloway 11 was eliminated from analysis of seasonal variation in pinfish diet.

Data were sufficient for seasonal analysis of diet in postlarval pinfish only at Econfina 12. Pinfish <16 mm SL were collected at this site from January through April. In January and February, postlarval pinfish consumed primarily calanoid copepods, plus a small number of invertebrate eggs. Later, they consumed harpacticoid copepods and amphipods in large quantities, and no calanoid copepods were taken by postlarvae in April. The relative abundance of calanoid copepods and invertebrate eggs in the diet of these fish coincided directly with the absolute abundance of the planktonic food items as determined by plankton tows taken on the day of fish collections. Copepods and invertebrate eggs were most abundant in January and February, and declined to annual lows in April (Table 3). Amphipod abundance remained relatively high at Econfina 12 through the winter and spring with annual minima occurring in the fall. Because amphipods were most abundant in January and February (Table 3), when copepod consumption was highest, it would appear that calanoid copepods are the preferred prey of postlarval pinfish. Only when calanoid populations fell to near zero did amphipods become a major portion of the diet.

Pinfish of the carnivorous feeding group (16-35 mm SL) were collected from March through August. In the spring and summer, amphipods and harpacticoid copepods were the primary dietary components of these fish (Figure 6). Clearly, however, amphipods were most important at Econfina 10. Amphipod consumption decreased with time and by late summer the primary dietary components were harpacticoid copepods and small shrimp. A small amount of plant material was taken at all three vegetated stations in midwinter. Invertebrate eggs and other animal foods consistently contributed small amounts to the diets of pinfish between 16 and 35 mm SL.

Temporal variations in diet of pinfish from 16 to 35 mm were analyzed by stepwise multiple regression using calanoid copepod, shrimp, amphipod, and benthic macrophyte abundance (Table 3) as independent variables. Amphipod consumption was positively correlated with amphipod abundance (except Econfina 10) and negatively related to plant, shrimp, and calanoid copepod abundance.

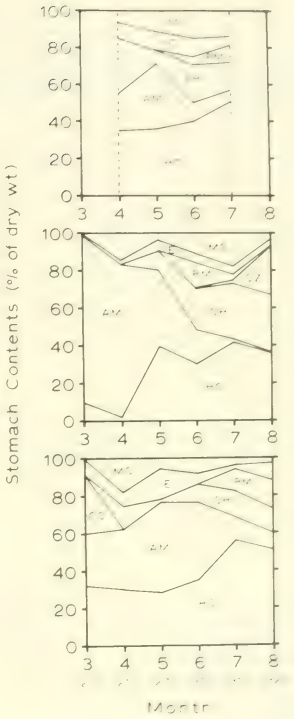


FIGURE 6.—Seasonality in diet of *Lagodon rhomboides* between 16 and 35 mm SL from three stations (F 12-top, E 10-middle, E 12-bottom) in Apalachee Bay, Fla. (March to August 1977). Diet is given as the relative proportion of the dry weight of stomach contents. Codes for the dietary components are given in Table 1. Numbers in parentheses are the mean lengths of fish.

At least 97.6% of the variation in amphipod consumption was explained by three independent variables for all three stations. Significant multiple correlation values for temporal variation in shrimp consumption were obtained for fish from Econfina 10 and 12 ($r^2 = 0.986$ and 0.999, respectively) (Table 4). Shrimp consumption was positively correlated with shrimp abundance, plant biomass, and calanoid copepod abundance. Negative relationships were found with amphipod abundance. Harpacticoid intake was positively related to plant biomass.

Pinfish between 36 and 80 mm SL were available year-round at vegetated sites and were considered to be omnivores. Examination of temporal

TABLE 4.—Pearson correlation coefficients (r) and coefficients of determination (r^2) for percentages of total stomach contents (dry weight) composed of: amphipods and shrimp in *Lagodon rhomboides* from 16 to 35 mm SL, tested as functions of food abundance. AM = amphipods/m², CC = calanoid copepods/m³, PM = grams dry weight benthic macrophytes/m², and SH = shrimp and shrimp postlarvae/m².

Fenholloway 12			Econfina 10			Econfina 12		
Step	r	r^2	Step	r	r^2	Step	r	r^2
			Amphipods consumed					
CC	-0.909	0.826	SH	-0.802	0.643*	AM	0.887	0.787*
SH	-0.234	0.995*	AM	-0.083	0.994**	SH	-0.716	0.866*
AM	0.482	n.s.	CC	-0.388	0.999**	PM	-0.090	0.976*
PM	-0.391		PM	-0.692	n.s.	CC	-0.792	n.s.
			Shrimp consumed					
CC	0.789	n.s.	SH	0.872	0.760*	AM	-0.825	0.681*
SH	0.318		AM	-0.066	0.972**	CC	0.231	0.868*
AM	-0.741		CC	0.257	0.986*	PM	0.662	0.998**
PM	-0.056		PM	0.604	n.s.	SH	0.783	n.s.

*$P \leq 0.05$; **$P \leq 0.01$; n.s. = not significant.

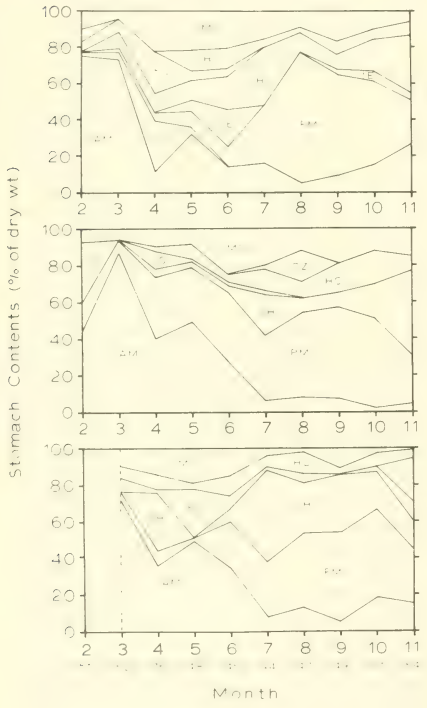


FIGURE 7.—Seasonality in diet of *Lagodon rhomboides* between 36 and 80 mm SL from three stations (F 12-top, E 10-middle, E 12-bottom) in Apalachee Bay, Fla. (February to November 1977). Diet is given as the relative proportion of the dry weight of stomach contents. Codes for the dietary components are given in Table 1. Numbers in parentheses are the mean lengths of fish.

variation in the diet of this ontogenetic group, however, showed that plant material made up only a small portion of the diet in winter and early spring (Figure 7). Amphipod consumption was highest in March and decreased through the spring and fall, during which time plant material became the most important food item. Consumption of shrimp and shrimp postlarvae was low in the spring but increased to as much as 30% of the diet in the summer and fall. Consumption of calanoid copepods by this fish size class was generally limited to winter. Harpacticoid copepods consistently contributed a small amount to the diet of these fish but consumption of isopods, crab zoea, and polychaetes was sporadic.

For fish from 36 to 80 mm, temporal variations in consumption of amphipods, plant matter, and shrimp were analyzed with stepwise multiple regression, using abundance of shrimp, amphipods, polychaetes, and benthic macrophytes as independent variables. Pearson correlation coefficients show that consumption of amphipods was negatively correlated with abundance of shrimp and macrophytes in the field and positively related to amphipod abundance (Table 5). The relationships with polychaete abundance were mixed. Multiple correlation coefficients explained between 60.8 and 79.4% of the temporal variation in amphipod consumption using from two to four independent variables. Consumption of plant matter by fish from 36 to 80 mm was positively related to plant biomass and shrimp abundance.

TABLE 5.—Pearson correlation coefficients (r) and coefficients of determination (r^2) for percentages of total stomach contents (dry weight) composed of: amphipods, plant matter, and shrimp in *Lagodon rhomboides* from 36 to 80 mm SL, tested as functions of food abundance. AM = amphipods/m², PO = polychaetes/m², PM = grams dry weight benthic macrophytes/m², and SH = shrimp and shrimp postlarvae/m².

Fenholloway 12			Econfina 10			Econfina 12		
Step	r	r^2	Step	r	r^2	Step	r	r^2
			Amphipods consumed					
SH	-0.561	0.315	SH	-0.802	0.643**	AM	0.616	0.380
AM	-0.462	0.500*	PM	-0.588	0.746**	SH	-0.126	0.664*
PO	0.105	0.608*	PO	-0.090	0.758*	PM	-0.574	n.s.
PM	-0.448	0.631*	AM	0.126	0.794*	PO	0.524	
			Plant matter consumed					
SH	0.639	0.408*	PM	0.912	0.831**	PO	-0.714	0.510
AM	0.105	n.s.	SH	0.594	0.912**	SH	0.214	0.652*
PO	-0.257		PO	-0.304	0.926**	AM	-0.694	0.786*
PM	0.428		AM	0.022	0.955**	PM	0.635	n.s.
			Shrimp consumed					
PO	-0.034	n.s.	PO	0.654	0.428*	PM	0.496	n.s.
AM	0.316		AM	0.013	0.667*	SH	-0.116	
PM	-0.218		SH	0.389	0.698*	AM	-0.388	
SH	0.024		PM	-0.401	0.741*	PO	-0.197	

*$P \leq 0.05$; **$P \leq 0.01$; n.s. = not significant.

Plant consumption was inversely related to polychaete field density at all three stations and relationships with amphipod abundance were mixed. Multiple regression did not provide a satisfactory model for variation in plant matter consumed at Fenholloway 12, but plant and food item abundances explained 78.6 and 95.5% of the variation at Econfina 12 and 10. Explanation of temporal variation in shrimp consumption by multiple regression methods was successful only for fish from Econfina 10 ($r^2 = 0.741$). Shrimp intake increased with shrimp abundance in the field and decreased with plant and polychaete abundances. Other correlations were low. Harpacticoid copepod consumption was positively related to plant biomass and negatively correlated with amphipod abundance; however, multiple correlation coefficients were not computed since no data were available on harpacticoid abundance.

Diet of large pinfish (>80 mm SL) showed little seasonality at Econfina 10, where plant material made up at least 80% of the stomach contents on all dates. At Fenholloway 12, however, benthic vegetation was less abundant than at Econfina 10 and major changes in diet occurred with season (Figure 8). Clearly, large pinfish were carnivorous during winter and early spring at Fenholloway 12, but became herbivorous in May. Winter diet included polychaetes, bivalves, amphipods, and isopods. Animal material was unimportant in the diets of fish taken during the rest of the year.

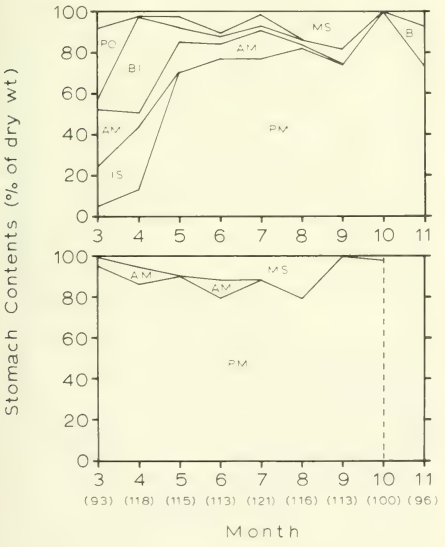


FIGURE 8.—Seasonality in diet of *Lagodon rhomboides* >80 mm SL from two stations (F 12-top, E 10-bottom) in Apalachee Bay, Fla. (March to November 1977). Diet is given as the relative proportion of the dry weight of stomach contents. Codes for the dietary components are given in Table 1. Numbers in parentheses are the mean lengths of fish.

Temporal variation in the diets of adult fish was not adequately explained with multiple regression, as obvious trends in plant consumption did not follow seasonal patterns in macrophyte abundance. Lack of temporal variation in diet at Econfina 10 is due to the fact that plants were readily available at that station when adult pinfish were present (March through October). On the other hand, at Fenholloway 12, macrophytes were patchy in distribution and a high biomass in April (Table 3) was composed largely of *T. testudinum* which was generally not consumed by pinfish. Abundance of alternative prey organisms, such as isopods and bivalves, may also explain carnivory of adult pinfish at Fenholloway in the spring.

Breadth of diet in pinfish was examined by calculating Shannon-Weiner diversity indices, H', and by tabulating the number of food items that individually contributed >1.0% of the total mass of stomach contents for each fish size class, sampling date, and station (Table 6, Figure 9). Dietary diversity of pinfish between 16 and 80 mm was lowest at the unvegetated site because two food items, amphipods and calanoid copepods, overwhelmed the importance of other foods. Low abundance of alternative prey such as shrimp, shrimp postlarvae, and benthic macrophytes probably explain this occurrence. For fish >80

TABLE 6.—Dietary diversity, H', and number of food types (individually contributing >1.0% of the total mass of stomach contents) in *Lagodon rhomboides* from four stations in Apalachee Bay, Fla. (mean ± SD). Within a fish size group, no mean values were significantly different (ANOVA and Duncan's multiple range test, $P>0.05$).

Size group (mm)	Fen 11	Fen 12	Econ 10	Econ 12
		Dietary diversity, H'		
11-15	—	—	0.57±0.39	0.54±0.64
16-35	0.99±0.50	1.68±0.17	1.28±0.59	1.45±0.13
36-80	1.27±0.46	1.68±0.44	1.64±0.44	1.58±0.25
>80	—	0.92±0.44	0.50±0.36	0.41±0.22
		Number of food types		
11-15	—	—	2.2±0.9	2.7±2.0
16-35	5.0±2.8	7.5±2.1	5.5±2.3	5.8±1.2
36-80	6.2±1.7	8.6±2.4	8.1±3.0	7.2±1.2
>80	—	6.2±2.3	4.4±1.7	4.5±0.7

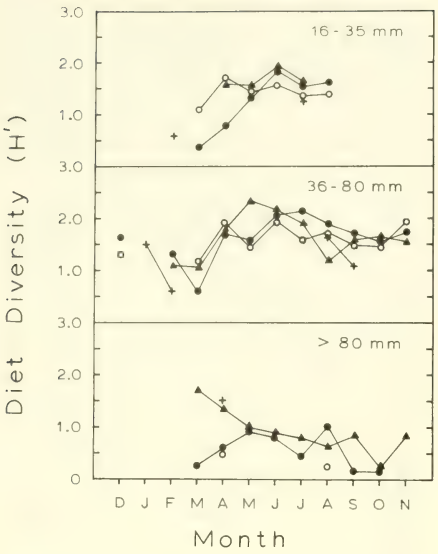


FIGURE 9.—Breadth of diet in *Lagodon rhomboides* from four sites in Apalachee Bay, Fla., shown as a function of season. Each value is the Shannon-Weiner index, H', for the food items consumed by fish of three size classes. Crosses = Fenholloway 11, triangles = Fenholloway 12, dots = Econfina 10, circles = Econfina 12.

mm, dietary diversity was highest at the sparsely vegetated station because, in addition to plant material, mussels, polychaetes, and other animal prey made an important contribution to the diet. At the Econfina stations, the diets of adult fish were dominated by plant material causing low dietary diversity.

Pinfish between 36 and 80 mm SL showed greatest breadth in diet; however, some degree of seasonality in dietary diversity occurred in all fish >15 mm (Figure 9). In fish between 16 and 35 mm, peak dietary breadth in June and July corresponded with periods of low amphipod abundance and a change in food habits to alternative prey types including shrimp and plant material. Lowest dietary breadth in fish between 36 and 80 mm occurred in the late winter and spring when amphipods were abundant and macrophyte biomass was low. Diversity of food items available was probably lowest at this time. Dietary diversity in fish >80 mm SL reflected the degree of carnivory by the fish. At Fenholloway 12 dietary diversity was highest in March and April when various animal foods were consumed in large quantities. At Econfina 10, highest diversity occurred in August when a large number of animal foods supplemented a normally herbivorous diet. During late spring and summer months, dietary diversity indices at Econfina 10 and Fenholloway 12 converged to similar values as fish at both stations became largely herbivorous. Very low dietary diversities occurred at Econfina 10 in September and October because over 98% of the diet was composed of plant material.

DISCUSSION

Pinfish from Apalachee Bay passed through five major ontogenetic feeding stages, including 1) planktivory; 2) carnivory on amphipods and harpacticoid copepods; 3) omnivory on amphipods, shrimp, and microepiphytes; 4) omnivory on epiphytes, amphipods, polychaetes, and isopods; and 5) herbivory on epiphytes and vascular plant material (primarily *S. filiforme*). Darnell (1958) and Carr and Adams (1973) provide the most reliable data for comparison with the present study on food habits of *L. rhomboides* since each provided information on ontogenetic variation in the diets of the fish. Darnell, studying stomachs of pinfish from Lake Ponchartrain, La., found that the importance of amphipods and other small crustaceans decreased with pinfish length (40-150 mm SL), while vegetable material became increasingly important in diet with fish size. Except that Darnell found dipterans to be a common food item in fish from Lake Ponchartrain, his findings were similar to mine. Pinfish collected near Crystal River, Fla., showed five trophic stages (Carr and Adams 1973); the stages were different from those reported here (Table 7). Unlike pinfish from Apalachee Bay, those from Crystal River became herbivores at an early stage (36-60 mm SL), and later showed strict carnivory on fish and shrimp (>80 mm SL). Fishes were rarely found in the stomachs of pinfish from Apalachee Bay and the pattern of increasing herbivory with fish length appeared to hold except at the unvegetated site where plant material was not available. Because stomach analyses for both geographical areas covered a full year, differences between the findings of the two studies cannot be attributed to artifacts introduced by seasonal variation in diet. Rather, it is likely that different abundances of suitable prey or plant items explain geographical differences in

TABLE 7.—Trophic ontogeny of pinfish collected at Crystal River and Apalachee Bay, Fla. Crystal River data were taken from Carr and Adams (1973).

Feeding stage	Size of fish (mm SL)
Crystal River	
1. Planktivore on copepods	10- 20
2. Carnivore on shrimp, mysids, and amphipods	26- 30
3. Herbivore on epiphytes	36- 60
4. Omnivore on epiphytes, shrimp, and fish	61- 80
5. Carnivore on shrimp and fish	81-110
Apalachee Bay	
1. Planktivore on copepods and invertebrate eggs	11- 15
2. Carnivore on amphipods and harpacticoids	16- 35
3. Omnivore on amphipods, harpacticoids, shrimp, and epiphytes	36- 80
4. Omnivore on epiphytes, amphipods, polychaetes, and isopods	81-120
5. Herbivore on epiphytes and vascular plants	>120

food habits just as food abundance explained local variations in food habits among stations in Apalachee Bay. Carr and Adams described their study site as dominated by *Ruppia maritima* and *Halodule wrightii*. In Apalachee Bay, benthic vegetation was dominated by *T. testudinum*; therefore differences in food habits of pinfish between the two areas, may be due to characteristics of the habitat other than prey abundances. For example: 1) the wide blades of *T. testudinum* may provide better refuge from predation for shrimp and other crustaceans than that provided by narrow blades of *R. maritima* and *H. wrightii*, and/or 2) the plant material near Crystal River was, in some way, unsuitable as food for large pinfish. Hansen (1969) also reported that plant material was the dominant food item of pinfish from dense *Thalassia* and *Ruppia* beds in Pensacola Bay, Fla., suggesting that some characteristic of *Thalassia* beds promotes herbivory in pinfish. Similar to the present study, Hansen found that seasonal variation in plant consumption was related to seasonal availability of benthic macrophytes.

Trophic ontogeny in pinfish can be explained in terms of fish morphology. Width and height of the mouth in the open position was linearally related to standard length of pinfish and increased body and mouth size permitted pinfish to capture a broader range of prey sizes (Stoner 1979a). The same characteristics undoubtedly explain increases in numbers of prey types associated with increasing body size in juvenile fish. Increasing range of prey sizes and types with fish body and mouth size has been reported by many authors (e.g., Wong and Ward 1972; Ware 1972, 1973; Ross 1978). Transition to herbivory by pinfish, first as a microepiphyte nibbler and later to a seagrass grazer is associated with changes in dentition with growth. Very fine conical jaw teeth only are found in fish at 15 mm SL, but conical teeth are replaced by longer caninelike teeth in fish between 23 and 35 mm. Conical and canine teeth are well adapted for capturing small animal prey, but chisel-shaped incisors, which appear in fish >35 mm, provide pinfish with the dentition required to graze plant material. Because of its dentition, the pinfish is probably an obligate carnivore until it reaches about 35 mm SL (for further discussion and illustration of ontogeny in pinfish dentition, see Caldwell 1957).

Given the morphological constraints of *L. rhomboides*, its reproductive seasonality is particularly well adapted for exploitation of food resources in seagrass meadows of Apalachee Bay. Postlarval pinfish entered the seagrass beds in midwinter at the time of peak abundance of calanoid copepods, appropriately small prey organisms. Winter spawning placed juvenile fish (16-35 mm) on the seagrass beds in the spring when the most valuable prey species, amphipods and harpacticoid copepods, were beginning to reproduce and reaching maximum abundance (Stoner[5]; Thistle[6]). Optimal prey for larger pinfish (36-80 mm) probably includes larger organisms such as shrimp which had peak abundance in the fall. Reproductive timing and growth placed large pinfish on the grass beds in the fall. The life history strategy of *L. rhomboides*, therefore, appears to be adapted to seasonal patterns of productivity and abundance in prey and macrophyte species. Although pinfish were among the fishes that were shown to influence the abundance of zooplankton in the Newport River estuary (Thayer et al. 1974), it is unlikely that pinfish postlarvae affect the abundance of calanoid copepods in Apalachee Bay because of the low number of pinfish postlarvae in the shallow bay (Brady 1980). However, pinfish probably do regulate the abundance of certain amphipod species in the bay (Stoner 1979a, b).

Variation in food habits with space, both on local and geographic scales, was a function of food availability and habitat structure. Food habits of fishes in Apalachee Bay were dramatically different at stations separated by distances as little as 2

[5]Stoner, A. W. 1980. Abundance, reproductive seasonality, and habitat preferences of amphipod Crustacea in seagrass meadows of Apalachee Bay, Florida. Manuscript in review.

[6]D. Thistle, Assistant Professor, Department of Oceanography, Florida State University, Tallahassee, FL 32306, pers. commun. December 1978.

km. At the station where vegetation and epibenthic prey organisms were sparse, pinfish took more food from the water column (e.g., copepods, chaetognaths, and polychaete larvae) than at other stations. Due to the lack of vegetable matter at this station, pinfish consumed *Brachidontes exustus* which lives on oyster bars near the unvegetated site. A high percentage of empty stomachs at the unvegetated site indicates that feeding conditions there were poor, especially for postlarval and adult pinfish. Although selection of food by fish is confounded by food preferences, the consumption of food by pinfish appears to reflect local, geographic, and seasonal abundances of the food organisms and the morphological limitations of the consumer.

Temporal variations in the food habits of *L. rhomboides* were well explained by abundance of prey types in the field, but the correlations were complex. Amphipod, shrimp, and plant consumptions were all directly related to the abundance of these primary food items in the field. Seasonal relationships between food abundance and consumption by fishes were observed by Lawler (1965), Repsys et al. (1976), and Hickey (1975). Diurnal changes in food habits have also been explained by changes in prey availabilities (Hobson and Chess 1976; Robertson and Howard 1978). Keast's (1970) observation that close correlation of prey availability with seasonality in food habits holds for only the most important prey types was also observed in this study. For example, polychaetes were relatively minor components of pinfish diets and showed no correlation with seasonal abundance patterns. On a statistical basis, however, absolute abundance of a food item in Apalachee Bay explained only part of the variation in consumption of that item. For example, although amphipod consumption by juvenile pinfish was directly related to amphipod abundance in the field, amphipod intake was also inversely related to shrimp and plant abundances. These inverse relationships were often stronger than the positive relationship with amphipod abundance. Similarly, shrimp consumption was negatively correlated with amphipod and plant abundances, suggesting that the relative abundance of preferred prey items may be as important as absolute abundance of any one type. The picture is further clouded by the fact that plant material, which serves as an important food source for pinfish >35 mm, is also an obvious component of the habitat that lends protection to many small prey species (Nelson 1978; Stoner 1979a). Two explanations for the increased plant consumption with benthic macrophyte biomass are plausible: 1) plant material is taken as a simple response to its abundance, and/or 2) *T. testudinum* blades provide amphipods, shrimp, and other animal prey with protection from fish predation and inhibit the consumption of these animals; therefore, as blade density or plant biomass increases, macrophytes and epiphytes are taken as alternative food. Both mechanisms are probably influential in the determination of food habits in pinfish; however, the latter hypothesis is probably the most important mechanism since cellulase activity is not found in the alimentary tract of *L. rhomboides* (Stickney and Shumway 1974). Densely vegetated seagrass habitats support greater densities and biomass of potential prey species than unvegetated or sparsely vegetated substrates (O'Gower and Wacasey 1967; Orth 1977; Brook 1978; Stoner in press), although is is unknown as yet whether this relationship is due to reduced predation on the animals or some property inherent in the structure of the habitat. The problem of omnivory in pinfish would be an especially fertile area for investigation in terms of optimal foraging theory, but a large array of carefully controlled field and laboratory experiments would be required.

Dietary specialization is generally found to be correlated with increasing food abundance. This conclusion is supported by models of predator-prey relationships (see review by Pyke et al. 1977) and empirical studies with fishes (Ivlev 1961; Zaret and Rand 1971; Werner and Hall 1974). On the basis of seasonal prey abundance patterns and the diets of pinfish between 16 and 80 mm SL, dietary specialization did occur with periods of high prey abundance. For example, at the vegetated stations amphipods and other macrobenthic organisms were most abundant between February and May. Lowest dietary diversities occurred during the same time period. With adult fish, however, the characteristic relationship did not seem to hold. Fenholloway 12 and Econfina 10 showed similar seasonal trends in abundance of food organisms yet seasonality of dietary diversity was entirely different at the two stations. Also, on a spatial basis, lowest dietary diversity occurred at the site with extremely low food abundance (Fenholloway 11) for fish between 16 and 80 mm SL. More generalized diets were found at the vegetated sites where food was more abundant. The predicted relationship of increasing dietary specialization

with increasing food abundance did not hold in certain instances because the abundance of macrobenthic organisms at the study site was closely related to standing crop of benthic macrophytes at the site (Stoner in press). Also, since seagrasses and epiphytes serve as important dietary components of larger pinfish, prediction of dietary diversity is further complicated.

Data provided in this study further verify the conclusion that *L. rhomboides* is a generalist feeder. Schoener (1969) suggested that generalist feeding strategy is favored when: 1) food density is low and there is a premium on the ability of the animal to take a range of prey, 2) the predator has a relatively long period to gain energy, and 3) prey densities fluctuate widely. Given the relatively low abundance of prey species in Apalachee Bay, the great diversity of potential prey items, and their high degree of variability with time and space, the generalist feeding strategy exhibited by *L. rhomboides* would be predicted by Schoener's model.

The detailed analysis of the food habits of *L. rhomboides* provided in this study accentuate difficulties inherent in the description of a trophic niche. Because of dramatic variation in food habits and dietary breadth in coastal fishes, serious methodological problems arise in description of food habits. In most cases, length-frequency distributions of fish are not constant with time; consequently, when animals are not placed in size classes or when placed in overly large size classes, dietary variation may be due to either seasonal changes in food habits or increasing fish size. The diet of a group of fish will be a function of the length-frequency distribution of the population if variation with size occurs. When food habits are examined by size and not by season, variation within a given size class may appear greater than is actually true at any particular time, and seasonality of diet is completely obscured. Variability in food habits as a function of space (a common occurrence) adds still one more dimension to the problem of describing an animal's food and feeding habits, but spatial variation is usually ignored. Keast (1970), in a study of the bioenergetic interrelationships of cohabiting freshwater fishes in Ontario, provided insight into the complex interactions of fish size and season in determining food habits. One other study (Nakashima and Leggett 1975), an investigation of responses of yellow perch to different levels of phytoplankton and benthic biomass in Lake Memphremagog, Quebec-Vermont, showed interactions of time and fish size in diet determination. The dimension of space was added by comparing the diets of fish from the northern and southern basins of the lake. Few studies have described more than one dimension of an animal's food habits.

Peters (1977) stated that the "Trophodynamic Concept" (Lindeman 1942) is based upon the premise that organisms in an ecosystem are categorized according to their distance along a food chain from the sun. He pointed out, however, that the real world is constructed of complex food webs and organisms do not fall into neat categories such as "primary consumer" or "secondary carnivores." This is not a new idea. In 1961, Darnell asserted that "trophic level" is an inoperational term since: 1) animals of a given size and belonging to a single species take food from several sources, 2) alternate foods are frequently utilized as a function of their availabilities, 3) an ontogenetic progression of food habits is common in animals, and 4) many animals are dependent upon detrital material which is itself of a complex origin and an undefined distance from primary producers. Regier and Henderson (1973) and Kercher and Shugart (1975) provided similar reasoning for the inadequacies of the trophic level concept. Darnell recommended a spectral approach to the food habit problem and Kercher and Shugart defined an "effective trophic position," actually a continuous index of trophic position rather than the conventional discrete level. Neither solution to the problem addressed all of Darnell's objections and gave an accurate portrayal of the functional role of the organism in its ecological context. Data provided in this paper show that, in addition to ontogenetic pattern in food habits, animals within given size classes take foods from several sources with the possible exception of postlarval pinfish which are collected only in the winter and early spring. Fish of many size classes consumed significant quantities of calanoid copepods which are probably herbivores; harpacticoid copepods which may be detritovores, herbivores, or carnivores; amphipods which show wide variety in food habits; plus shrimp, invertebrate eggs, and many other invertebrate taxa. In most cases, the prey species themselves cannot reliably be placed in any one trophic level and, since individuals of a given species were consumed at different developmental stages, and prey species may show trophic ontogeny, the problem of assigning a trophic level to the predator is further

confounded. Pinfish >35 mm SL nearly always contained both plant and animal material in their stomachs. Omnivory, of course, automatically makes the fish both a "primary" and "secondary consumer." Darnell's (1961) suggestion that predators commonly utilize food resources according to their availabilities was clearly demonstrated in this paper as it related to other spatial and temporal patterns of food abundance in Apalachee Bay. Although pinfish do not rely directly on detrital material as a source of nutrition, many of its prey organisms do (e.g., certain harpacticoid copepods, amphipods, shrimps, and polychaetes). Because it is difficult to place detritovores in trophic levels, the predatory fish also falls within no discrete level. On these bases, the trophic level concept is rendered inoperational for relationships involving the dominant epibenthic fish in Apalachee Bay. Furthermore, because of migration of consumers and wide variation in food habits with season and consumer growth, one may never assume that food webs, predator-prey relationships, or the functional role of a predator are static. The taxonomic species is not, in many cases, a functional ecological unit. At the very least, ontogenetic feeding groups should be incorporated in ecological models. These "trophic units" would be particularly useful where the true ecological role of the animal in a model is important. Except in the most simple food webs, without precise knowledge of variation in food habits and diet breadth, models of energetic pathways and predator-prey relationships and measurement of niche breadth and overlap will be accurate neither in theory nor in practice.

Characteristics of prey species which mediate predation include absolute and relative abundances, conspicuousness, size, palatability, defensive morphology and behavior, spatial distribution including microhabitat and aggregation, and nutritional value. All of the above, however, are limited or mediated by various elements of the environment including temperature, turbidity, dissolved oxygen, light, water motion, and structural aspects of the habitat. Although a great deal of research has been conducted concerning the importance of predator and prey characteristics, most of the work has been done in structurally simple systems, including mud bottom, freshwater pond, and water column habitats where the number of food species is relatively low. Data from this and another paper (Stoner 1979b) show that seagrass blades and rhizomes provide a very important structural component in seagrass meadows which affect both predator and prey species and their interactions. Since seagrass biomass, blade densities, and species compositions vary over both time and space, plant-animal and predator-prey relationships are in constant flux. The seagrass habitat, therefore, is an extremely complex system within which the ecological roles of predation and habitat structure are ever changing. The need for further investigation is obvious.

ACKNOWLEDGMENTS

This research was supported by grant number R-805288010 from the U.S. Environmental Protection Agency to Robert J. Livingston. I wish to thank all of those graduate and undergraduate students who helped with field collections. E. L. Bousfield, H. Greening, H. Kritzler, F. G. Lewis, S. L. Santos, P. F. Sheridan, and J. L. Simon provided assistance with the taxonomy of various benthic organisms. Aid with computer programming and statistical procedures was generously provided by G. C. Woodsum and D. Zahn. L. G. Abele, W. F. Herrnkind, R. A. Laughlin, K. M. Leber, F. G. Lewis, R. J. Livingston, R. W. Menzel, R. W. Yerger, and an anonymous reviewer helped to point out several inconsistencies in the manuscript at various stages.

LITERATURE CITED

ADAMS, S. M.
1976. The ecology of eelgrass, *Zostera marina* (L.), fish communities. I. Structural analysis. J. Exp. Mar. Biol. Ecol. 22:269-291.

BELL, J. D., J. J. BURCHMORE, AND D. A. POLLARD.
1978a. Feeding ecology of a scorpaenid fish, the fortescue, *Centropogon australis*, from a *Posidonia* seagrass habitat in New South Wales. Aust. J. Mar. Freshwater Res. 29:175-185.
1978b. Feeding ecology of three sympatric species of leatherjackets (Pisces: Monacanthidae) from a *Posidonia* seagrass habitat in New South Wales. Aust. J. Mar. Freshwater Res. 29:631-643.

BRADY, K. D.
1980. An ichthyoplankton survey of Apalachee Bay, Florida. M.S. Thesis, Florida State Univ., Tallahassee.

BROOK, I. M.
1978. Comparative macrofaunal abundance in turtlegrass (*Thalassia testudinum*) communities in south Florida characterized by high blade density. Bull. Mar. Sci. 28:212-217.

CALDWELL, D. K.
1957. The biology and systematics of the pinfish, *Lagodon rhomboides* (Linnaeus). Bull. Fla. State Mus., Biol. Sci. 2:77-173.

CARR, W. E. S., AND C. A. ADAMS.
1972. Food habits of juvenile marine fishes: evidence of the cleaning habit in the leatherjacket, *Oligoplites saurus*, and the spottail pinfish, *Diplodus holbrooki*. Fish. Bull., U.S. 70:1111-1120.
1973. Food habits of juvenile marine fishes occupying seagrass beds in the estuarine zone near Crystal River, Florida. Trans. Am. Fish Soc. 102:511-540.

DARNELL, R. M.
1958. Food habits of fishes and larger invertebrates of Lake Ponchartrain, Louisiana, an estuarine community. Publ. Inst. Mar. Sci., Univ. Tex. 5:353-416.
1961. Trophic spectrum of an estuarine community based on studies of Lake Ponchartrain, Louisiana. Ecology 42:553-568.

FELLER, R. J., AND V. W. KACZYNSKI.
1975. Size selective predation by juvenile chum salmon (*Oncorhynchus keta*) on epibenthic prey in Puget Sound. J. Fish. Res. Board Can. 32:1419-1429.

HANSEN, D. J.
1969. Food, growth, migration, reproduction, and abundance of pinfish, *Lagodon rhomboides*, and Atlantic croaker, *Micropogon undulatus*, near Pensacola, Florida, 1963-65. U.S. Fish. Wildl. Serv., Fish. Bull. 68:135-146.

HICKEY, C. R., JR.
1975. Fish behavior as revealed through stomach content analysis. N.Y. Fish Game J. 22:148-155.

HOBSON, E. S.
1974. Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. Fish. Bull., U.S. 72:915-1031.

HOBSON, E. S., AND J. R. CHESS.
1976. Trophic interaction among fishes and zooplankters near shore at Santa Catalina Island, California. Fish. Bull., U.S. 74:567-598.

HOESE, H. D., AND R. S. JONES.
1963. Seasonality of larger animals in a Texas turtle grass community. Publ. Inst. Mar. Sci., Univ. Tex. 9:37-47.

IVLEV, V. S.
1961. Experimental ecology of the feeding of fishes. Yale Univ. Press, New Haven, Conn., 302 p.

KEAST, A.
1970. Food specializations and bioenergetic interrelations in the fish faunas of some small Ontario waterways. *In* J. H. Steele (editor), Marine food chains, p. 377-411. Univ. Calif. Press, Berkeley.
1979. Patterns of predation in generalist feeders. *In* H. Clepper (editor), Predator-prey systems in fisheries management: international symposium on predator-prey systems in fish communities and their role in fisheries management, Atlanta, Georgia, July 24-27, 1978, p. 243-355. Sport Fishing Inst., Wash., D.C.

KEAST, A., AND L. WELSH.
1968. Daily feeding periodicities, food uptake rates, and dietary changes with hour of day in some lake fishes. J. Fish. Res. Board Can. 25:1133-1144.

KERCHER, J. R., AND H. H. SHUGART, JR.
1975. Trophic structure, effective trophic position, and connectivity in food webs. Am. Nat. 109:191-206.

KJELSON, M. A., D. S. PETERS, G. W. THAYER, AND G. N. JOHNSON.
1975. The general feeding ecology of postlarval fishes in the Newport River estuary. Fish. Bull., U.S. 73:137-144.

LAWLER, G. H.
1965. The food of the pike, *Esox lucius*, in Heming Lake, Manitoba. J. Fish. Res. Board Can. 22:1357-1377.

LINDEMAN, R. L.
1942. The trophic-dynamic aspect of ecology. Ecology 23:399-418.

LIVINGSTON, R. J., R. S. LLOYD, AND M. S. ZIMMERMAN.
1976. Determination of sampling strategy for benthic macrophytes in polluted and unpolluted coastal areas. Bull. Mar. Sci. 26:569-575.

LOVE, M. S., AND A. W. EBELING.
1978. Food and habitat of three switch-feeding fishes in the kelp forests off Santa Barbara, California. Fish. Bull., U.S. 76:257-271.

MATUSITA, K.
1955. Decision rules, based on the distance, for problems of fit, two samples, and estimation. Ann. Math. Stat. 26:631-640.

NAKASHIMA, B. S., AND W. C. LEGGETT.
1975. Yellow perch (*Perca flavescens*) biomass responses to different levels of phytoplankton and benthic biomass in Lake Memphremagog, Quebec-Vermont. J. Fish. Res. Board Can. 32:1785-1797.

NELSON, W. G.
1978. Organization of a subtidal seagrass amphipod guild: the roles of predation, competition, and physical stress. Ph.D. Thesis, Duke Univ., Durham, 223 p.

O'GOWER, A. K., AND J. W. WACASEY.
1967. Animal communities associated with *Thalassia*, *Diplanthera*, and sand beds in Biscayne Bay. I. Analysis of communities in relation to water movements. Bull. Mar. Sci. 17:175-210.

ORTH, R. J.
1977. The importance of sediment stability in seagrass communities. *In* B. C. Coull (editor), Ecology of marine benthos, p. 281-300. Belle W. Baruch Library in Marine Science 6. Univ. S.C. Press, Columbia.

PETERS, D. S., AND M. A. KJELSON.
1975. Consumption and utilization of food by various postlarval and juvenile fishes of North Carolina estuaries. *In* L. E. Cronin (editor), Estuarine research, Vol. 1, p. 448-472. Acad. Press, N.Y.

PETERS, R. H.
1977. The unpredictable problems of trophodynamics. Environ. Biol. Fishes 2:97-101.

PYKE, G. H., H. R. PULLIAM, AND E. L. CHARNOV.
1977. Optimal foraging: A selective review of theory and tests. Rev. Biol. 52:137-154.

REGIER, H. A., AND H. F. HENDERSON.
1973. Towards a broad ecological model of fish communities and fisheries. Trans. Am. Fish. Soc. 102:56-72.

REISE, K.
1978. Experiments on epibenthic predation in the Wadden Sea. Helgol. wiss. Meeresunters. 31:55-101.

REPSYS, A. J., R. L. APPLEGATE, AND D. C. HALES.
1976. Food and food selectivity of the black bullhead, *Ictalurus melas*, in Lake Poinsett, South Dakota. J. Fish. Res. Board Can. 33:768-775.

ROBERTSON, A. I., AND R. K. HOWARD.
1978. Diel trophic interactions between vertically-migrating zooplankton and their fish predators in an eelgrass community. Mar. Biol. (Berl.) 48:207-213.

ROSS, S. T.
1978. Trophic ontogeny of the leopard searobin, *Prionotus scitulus* (Pisces: Triglidae). Fish. Bull., U.S. 76:225-234.

SCHOENER, T. W.
1969. Optimal size and specialization in constant and fluc-

tuating environments: an energy-time approach. Brookhaven Symp. Biol. 22:103-114.

SHERIDAN, P. F.
1978. Trophic relationships of dominant fishes in the Apalachicola Bay system, Florida. Ph.D. Thesis, Florida State Univ., Tallahassee, 216 p.

STEIN, R. A.
1977. Selective predation, optimal foraging, and the predator-prey interaction between fish and crayfish. Ecology 58:1237-1253.

STICKNEY, R. R., AND S. E. SHUMWAY.
1974. Occurrence of cellulase activity in the stomachs of fishes. J. Fish. Biol. 6:779-790.

STONER, A. W.
1979a. The macrobenthos of seagrass meadows in Apalachee Bay, Florida, and the feeding ecology of *Lagodon rhomboides* (Pisces: Sparidae). Ph.D. Thesis, Florida State Univ., Tallahassee, 175 p.
1979b. Species specific predation on amphipod crustacea by pinfish (*Lagodon rhomboides*): Mediation by macrophyte standing crop. Mar. Biol. (Berl.) 55:201-207.
In press. The role of seagrass biomass in the organization of benthic macrofaunal assemblages. Bull. Mar. Sci.

THAYER, G. W., D. E. HOSS, M. A. KJELSON, W. F. HETTLER, JR., AND M. W. LACROIX.
1974. Biomass of zooplankton in the Newport River estuary and the influence of postlarval fishes. Chesapeake Sci. 15:9-16.

VAN BELLE, G., AND I. AHMAD.
1974. Measuring affinity of distributions. *In* F. Proschan and R. J. Serfling (editors), Reliability and biometry: statistical analysis of lifelength: papers, p. 651-668. Soc. Ind. Appl. Math., Phila.

WARE, D. M.
1972. Predation by rainbow trout (*Salmo gairdneri*): the influence of hunger prey density, and prey size. J. Fish. Res. Board Can. 29:1193-1201.
1973. Risk of epibenthic prey to predation by rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 30:787-797.

WERNER, E. E., AND D. J. HALL.
1974. Optimal foraging and the size selection of prey by bluegill sunfish (*Lepomis macrochirus*). Ecology 55:1042-1052.

WONG, B., AND F. J. WARD.
1972. Size selection of *Daphnia pulicaria* by yellow perch (*Perca flavescens*) fry in West Blue Lake, Manitoba. J. Fish. Res. Board Can. 29:1761-1764.

YOUNG, D. K., M. A. BUZAS, AND M. W. YOUNG.
1976. Species densities of macrobenthos associated with seagrass: A field experimental study of predation. J. Mar. Res. 34:577-592.

YOUNG, D. K., AND M. W. YOUNG.
1977. Community structure of the macrobenthos associated with seagrass of the Indian River estuary, Florida. *In* B. C. Coull (editor), Ecology of marine benthos, p. 359-381. Belle W. Baruch Library in Marine Science 6. Univ. S.C. Press, Columbia.
1978. Regulation of species densities of seagrass-associated macrobenthos: Evidence from field experiments in the Indian River estuary, Florida. J. Mar. Res. 36:569-593.

ZARET, T. M., AND A. S. RAND.
1971. Competition in tropical stream fishes: Support for the competitive exclusion principle. Ecology 52:336-342.

ZIMMERMAN, M. S., AND R. J. LIVINGSTON.
1976a. Effects of kraft mill effluents on benthic macrophyte assemblages in a shallow-bay system (Apalachee Bay, north Florida, USA). Mar. Biol. (Berl.) 34:297-312.
1976b. Seasonality and physico-chemical ranges of benthic macrophytes from a north Florida estuary (Apalachee Bay). Contrib. Mar. Sci. 20:33-45.

OBSERVATIONS ON A MASS STRANDING OF SPINNER DOLPHIN, *STENELLA LONGIROSTRIS*, FROM THE WEST COAST OF FLORIDA

JAMES G. MEAD,[1] DANIEL K. ODELL,[2] RANDALL S. WELLS,[3] AND MICHAEL D. SCOTT[4]

ABSTRACT

The spinner dolphin, *Stenella longirostris*, while well known in portions of the Pacific Ocean, has rarely been available for study in the Atlantic. Data from 28 individuals from a mass stranding in Florida enabled us to make preliminary estimates of mean size and age at sexual and physical maturity, reproductive seasonality, and sexual dimorphism for this species in the southwest Atlantic. Our sample most closely resembles the Hawaiian populations described by Perrin, but further work in the Atlantic is likely to demonstrate other populations differing morphologically from this one.

The spinner dolphin, *Stenella longirostris*, is widely distributed in tropical to warm temperate waters of the world (Perrin 1975), but due to its predominately pelagic habits, is seldom found stranded and is not generally taken in coastal fisheries. As a result, very little is known of its biology except in the eastern tropical Pacific, where it is taken in considerable numbers incidental to purse seining for yellowfin tuna. Perrin et al. (1977) have recently published investigations on the eastern population of spinner dolphin from the Pacific.

The species is apparently common in the Caribbean (Caldwell et al. 1971; Erdman et al. 1973; Taruski and Winn 1976), but there are few records, all of them strandings, from the Gulf of Mexico. Gunter (1954) did not find any evidence of this species in the Gulf of Mexico. Layne (1965) reported on a mass stranding of this species from Dog Island, Fla. (lat 29°48′ N, long. 84°38′ W), where 36 animals stranded on September 1961. Lowery (1974) reported a single adult male from Fort Walton Beach, Fla. (lat. 30°24′ N, long. 84°47′ W). Schmidley and Shane[5] reported a 158 cm male which stranded alive at Sabine Pass Beach, Tex., on 16 May 1976, and a pregnant 188 cm female found on Padre Island, Tex., during March 1975. Shane (1977) reported two additional records from Padre Island: a 173 cm female which stranded about January 1976 and a 183 cm male on 4 June 1977. The present study is based on 28 animals from a single mass stranding on the west coast of Florida.

At this point it is not possible to determine whether the occurrences recorded from the west coast of Florida were derived from a population in the Gulf of Mexico or were strays from the Caribbean. While there is a small fishery for mixed species of dolphins in the Caribbean (Caldwell et al. 1971), catches of spinner dolphin are relatively infrequent and are unlikely to have an appreciable effect on the population. In contrast, the populations studied by Perrin and others in the Pacific are taken in large numbers incidental to purse seining for yellowfin tuna.

The causes of mass strandings of cetaceans are still very little understood (see Geraci 1978 for a recent review of the subject). It is clear that this is a very complex problem which goes far beyond the scope of this paper. It is also clear that much of our lack of understanding is based upon a lack of information on the species involved. We have felt that it was also important to include material on the circumstances of the stranding itself, even though this is not directly related to the conclusions drawn from examination of the specimens.

CIRCUMSTANCES OF THE STRANDING

The stranding occurred on the north end of Casey Key, with most of the dolphins concentrated

[1]Division of Mammals, Smithsonian Institution, Washington, DC 20560.

[2]Rosensteil School of Marine and Atmospheric Sciences, University of Miami, Miami, FL 33149.

[3]Department of Zoology, University of Florida, Gainesville, Fla.; present address: Center for Coastal Marine Studies, University of California, Santa Cruz, CA 95060.

[4]National Fish and Wildlife Laboratory, Gainesville, FL 32601.

[5]Schmidley, D. F., and S. H. Shane. 1978. A biological assessment of the cetacean fauna of the Texas coast. Final Rep., U.S. Marine Mammal Commission Contract MM4AC008, available Natl. Tech. Inf. Serv., Springfield, Va., as PB 281763, 38 p.

Manuscript accepted October 1979.
FISHERY BULLETIN: VOL. 78, NO. 2, 1980.

at about lat. 27°12′10″ N, long. 82°30′30″ W (Figure 1). The animals began coming ashore about 2200 h e.d.t. on the evening of 13 July 1976. At that time the wind was westerly at 10-15 mi/h, seas were running about 2 ft, and there was an extreme low tide at 2211 h. Upon discovering the animals, local residents attempted to direct them back to sea or move them to more sheltered areas.

Most observers concurred that there was a great deal of noise coming from all of the dolphins when they first came ashore, including much "squealing and crying," but that this later subsided. The animals were quite passive on the beach, with the exception of one large animal that reacted violently to handling and died during the short trip to Midnight Pass. Most of the dolphins did not resist handling and were easily walked to the shallow sand bar 10-15 m from shore, where they were pointed seaward, held until they began rhythmic swimming motions, and then given a push offshore. This was believed to be successful with some of the animals, but in many cases they would turn towards the south with the first wave that came over the bar and be washed back onto shore.

Eight to 10 animals, one of which was marked on the dorsal fin with a cattle ear tag, were moved to the more sheltered waters of Midnight Pass and released in there. A single small animal (possibly 504457)[6] was released in Little Sarasota Bay. The last live animal to come ashore with the initial stranding was 504449 which was found at 0130 h and died while attempts were being made to direct it back to sea. Estimates of the total number of animals ranged from 50 to 150, with most of the observers agreeing on the lower number.

Early morning of 14 July, four large animals and a calf stranded just north of Turtle Beach on Siesta Key, about 2 km north of the original stranding. Three of the large animals were directed back to sea, one died on the beach and was subsequently lost, and the calf (504459) was moved to Turtle Lagoon where it died. All of the live animals were off of the beach by 0800 h.

Later that morning, two live animals were picked up, one from the northeast end of Casey Key along the Intracoastal Waterway, and one from the grass beds just east of Bird Keys. The animal which had been tagged the night before (504434) was recovered dead from the latter area. Both of the live animals were probably from the group that had been transported and released at Midnight Pass. The live animals were held in an impoundment at the Mote Marine Laboratory on Siesta Key until they were picked up by Sea World and transported to holding facilities at Orlando, Fla., on 15 July. One of these (504456) died the next day; the other (504455) died 4 days later. A dead calf (504458) was recovered from the southern tip of Siesta Key, a dead adult (504451) was picked up on the west side of Bird Keys, and the accumulation of dead animals at the original stranding site on Casey Key was recovered and put on ice at the Mote Marine Laboratory on 14 July.

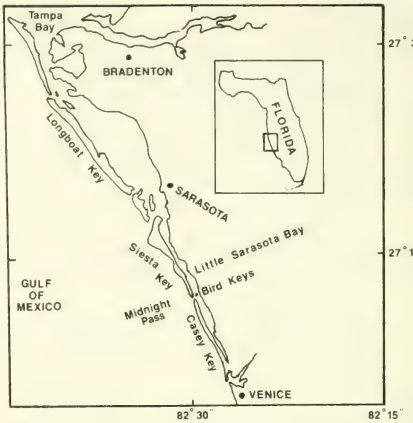


FIGURE 1.—Central west coast of Florida localities involved in the mass stranding of spinner dolphin.

Late afternoon of 15 July, we received notification that a small dolphin had been seen in the Intracoastal Waterway near marker no. 23 about 6 km south of Midnight Pass. This animal (504457) was found just after dark swimming slowly near shore and whistling loudly. It was picked up alive, but died early the next morning while being transported to Orlando. This was probably the calf which had been released in Little Sarasota Bay on 13 July.

The last animal to be recovered was the decomposed carcass of an adult male that was picked up on 16 July from Casey Key (504460).

An aerial survey was flown in a U.S. Coast Guard helicopter from 1800 to 2000 h on 14 July and on the afternoon of 16 July. No animals other than the dead ones on the beach were seen. The

[6]The six digit numbers used to identify the animals are catalog numbers of the United States National Museum, where the skeletal remains have been deposited.

stranding received a great deal of publicity from the news media, and it would be expected that we would have been notified if any additional animals had turned up on the coast.

Most of the dolphins bore minor abrasions that were probably incurred while stranding. Only one (504448) exhibited any appreciable physical damage. This animal, the largest male of the group, had two large shark bites on the left flank at about midlength and a third which completely removed the left fluke. These bites appeared to have been inflicted after death.

NECROPSY

One specimen was necropsied late on the evening of 14 July, the others on 15 July. The two animals which were transported to Sea World were necropsied on 16 and 20 July by the Sea World staff. A variety of lesions were observed in the sample necropsied on 15 July. Most were parasitic and not serious enough to account for death. The blubber layer appeared thin, but this was due at least in part to postmortem changes in the hot sun and measurements were not taken.

The stomachs of all specimens except the three calves were empty. Nicholas Hall (Department of Neuropathology, University of Florida, Gainesville, FL 32601) collected the brains from the animals necropsied on 15 July for neuropathological examination. Helminth parasites were collected and forwarded to Donald Forrester (Laboratory of Wildlife Disease Research, University of Florida, Gainesville, FL 32611). Gonad samples were collected and later analyzed at the Smithsonian Institution by Mead. Teeth were taken from all of the animals except the calves and were sectioned at about 175 μm in thickness by Odell using a Buehler Isomet Low Speed Saw[7], and were read for age determination by Odell and Mead. External measurements were taken by Wells and Scott while the animals were still on the beach, and organ weights were taken during the necropsies. Copies of all the measurements and necropsy data are in the Marine Mammal Program files (Division of Mammals, Smithsonian Institution, Washington, DC 20560). Skeleton materials from the specimens are being studied by William F. Perrin (Southwest Fisheries Center, NMFS, NOAA, La Jolla, CA 92038).

[7]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

REPRODUCTIVE DATA

The female reproductive tracts were removed, flat diameter of uterine horns measured at their midlength, ovaries collected and fixed, uterus opened and examined for fetuses, and mammary glands checked for gross indications of lactation. The ovaries were examined for externally visible corpora, indications of large maturing follicles, and were weighed. The ovaries were subsequently sectioned by William F. Perrin, providing confirmation of the external examination and an exact count of the corpora albicantia. None of the animals were visibly pregnant and only one (504456) was lactating. For practical purposes, females were considered sexually mature if there were external indications of at least one corpus on the ovaries. There was only one individual (504440) in which there was a discrepancy between the results of the external ovarian examination and the sectioning (Table 1). In this case a large follicle was probably mistaken for a corpus albicans on external examination.

The smallest sexually mature female was 187 cm long, and the largest immature female was 190 cm long. A 177 cm female showed no indications of follicular development, while four animals between 180 and 186 cm showed external indications of maturing follicles. The diameter of the larger of the two uterine horns showed a considerable increase (about twofold) at sexual maturity.

The good correspondence between ovarian condition and diameter of the uterine horns indicates that the latter may be a useful character for defining sexual maturity, as it is probably the result of pregnancy.

It seems likely that females begin to mature at about 180 cm and reach sexual maturity at a length of about 188 cm and a weight of about 55 kg. The 188 cm pregnant female reported by Schmidley and Shane (see footnote 5) fits this interpretation.

Considering only those females in which the pulp cavity of the tooth was open and for which an exact count of growth layer groups[8] could be made, there were four sexually immature animals, with a mean of 8.25 growth layer groups (7, 8, 8, and 10 groups), and three sexually mature animals, with a mean of 10 groups (7, 11, and 12 groups). Al-

[8]Terminology adopted at International Workshop on Determining Age of Odontocete Cetaceans, 8-19 September 1978, Southwest Fisheries Center, NMFS, NOAA, La Jolla, Calif.

TABLE 1.—Reproductive data on female spinner dolphin stranded in Florida. Epiphyses: 0 = open; 1 = closed; 2 = fused. Sexual maturity: 0 = mature; 1 = maturing; 2 = mature. Ages are in number of dentinal growth layer groups with + signifying that the pulp cavity was closed and the age was greater than the number of visible groups. The right and left ovaries were confused on 504437. However, they are presumed to correspond to the relative diameter of the uterine horns.

USNM number	Length (cm)	Weight (kg)	Age	Epiphyses	Gonad weight (g)		Uterine diameter (cm)		Ovarian corpora		Sexual maturity
					Right	Left	Right	Left	Right	Left	
504438	177	49	10	0	0.81	0.76	1.5	1.5	0	0	0
504450	180	54	8	0	0.48	1.47	1.5	1.5	0	0	1
504449	181	46.1	7	0	0.45	1.36	1.4	1.5	0	0	1
504453	183	47.5	8	0	0.50	1.08	1.5	1.5	0	0	1
504454	186	54	7	0	0.29	1.02	1.2	1.2	0	0	1
504441	187	55.3	8+	0	1.16	4.29	2.0	2.8	0	4	2
504444	189	53	11+	0	0.37	1.58	1.8	1.3	0	0	1
504440	190	56	7	0	0.81	1.85	1.3	1.6	0	0	1
504437	195	61.1	12	0	0.95	6.3+	1.9	3.0	0	1	2
504433	196	60.3	6+	1	1.39	1.99	1.9	2.3	0	7	2
504445	197	64	—	0	1.57	2.46	1.6	2.0	0	1	2
504451	201	65.2	11	2	1.22	5.11	2.9	3.0	0	9	2
504456	204	59	—	—	1.55	4.5	—	—	—	—	2

though sample size is small, it gives a useful preliminary estimate of age at sexual maturity of 7-10 growth layer groups (7-10 yr, see Perrin et al. 1976, 1977 for discussion of alternative growth layer-age relationships).

Comparable figures were given by Perrin et al. (1977) for the eastern spinner dolphin from the Pacific. They found a mean length at sexual maturity of 165 cm which is appreciably shorter than the estimate for this sample (188 cm). This is due at least in part to the eastern spinner dolphin being a relatively smaller animal (mean length of sexually mature females was 171 cm, whereas it was 197 cm for this sample). Perrin et al. (1977) found that mean age at sexual maturity was 5.5 growth layer groups, which may represent a decrease in age at sexual maturity as a result of fishing pressure on the eastern spinner population. This also might contribute to the shorter length at sexual maturity in that population.

As appears to be the case with many delphinids, there was a marked dominance of the left side of the reproductive tract (Harrison et al. 1972). In all of the mature or maturing animals, the left ovary was decidedly larger than the right, and only one animal (504441) bore any externally visible corpora on the right ovary. There was a corresponding asymmetry in the size of the uterine horns, with the left being equal to or larger than the right in all but one animal (504444), indicating that the greater number of pregnancies were carried in the left horn.

The testes were measured, weighed with the epididymis removed, and a sample taken for histological examination. Sections of testis samples were cut at 10 μm, stained with hematoxylin and eosin, and the diameter of the seminiferous tubules measured with an ocular micrometer. The tubules were randomly selected for examination, but only those approaching a direct rather than an oblique cross section and free from obvious artifacts of sectioning or decomposition were chosen for measurement. The least diameter was measured and the results given in Table 2 are the mean of 10 tubules, at a depth of about 1 cm from the surface of the testis. Tubules were also mea-

TABLE 2.—Reproductive data on male spinner dolphin stranded in Florida. Epiphyses: 0 = open; 1 = closed; 2 = fused. Sperm in epididymis: 0 = none; 1 = present; 2 = copious. Testis activity: 0 = no spermatogenesis; 2 = active spermatogenesis. Sexual maturity: 0 = immature; 1 = maturing; 2 = mature. Ages are in number of dentinal growth layer groups, with + signifying that the pulp cavity was closed and the age was greater than the number of visible layers.

USNM number	Length (cm)	Weight (kg)	Age	Epiphyses	Gonad weight (g)		Gonad length (cm)		Sperm in epididymis	Testis activity	Tubule diameter	Sexual maturity
					Right	Left	Right	Left				
504434	188	51	7	0	18	17	11	10	0	0	62	0
504435	189	55.8	7	0	250	220	24	20	0	1	136	1
504455	190	63.6	8+	—	320	310	—	—	1	—	—	1
504439	192	65.5	9+	1	730	720	32	30	—	1	244	2
504436	194	65.3	10	0	400	430	23	24	2	1	185	2
504442	195	60	10	—	—	460	27	27	1	1	180	2
504443	197	68	9+	1	560	550	27	25	1	1	200	2
504447	197	63.8	7+	0	96.5	100	15	16	1	0	80	0
504446	201	75	9+	2	860	870	31	32	2	1	196	2
504452	203	63.6	9+	—	500	500	27	27	1	1	173	2
504448	208	69+	8+	1	980	870	36	35	2	—	—	2

sured near the surface of the testis and it was noted that tubule diameter averaged about 10% less at that level in the mature males. The process of selection of the tubules for measurement may have introduced a slight bias in favor of smaller tubules, as these are possibly less likely to have been affected by decomposition artifacts. Much of the variation in tubule diameter within an individual slide may have been the result of autolytic distortion, which would tend to increase the diameter of the tubules.

There is a sharp increase in the size of the testes of animals with length of 188 or 189 cm (Table 2), which apparently is the size range at which maturation of the testes begins. Spermatogenesis was taking place in the testes of the 189 cm individual, but the testes weights were still low relative to those of fully mature animals and no sperm was present in the epididymis. In the next largest animal (190 cm), the testes were slightly larger and sperm was present in the epididymis, indicating that this animal was functionally sexually mature. All of the animals above 190 cm had large, active testes and were sexually mature, with the exception of a single 203 cm individual (504452), whose testes were markedly small, though there was a slight indication of spermatogenesis. The body weight of this animal was also low for its length, and it is probable that it was an abnormal individual.

Although the sample of males was too small to statistically define sexual maturity, it seems likely that maturation begins around a body length of about 190 cm and a weight of about 60 kg, and maturity is reached at a length of about 192 cm and a weight of about 65 kg. Animals with a seminiferous tubule diameter of less than about 150 μm were immature or maturing, and those with a diameter in excess of this were sexually mature. The corresponding figures for testis weight and length were about 300 g and 24 cm. The sample of males with the pulp cavity open in the teeth consists of only four specimens. One of these did not have well-defined growth layers, leaving only three usable individuals. These are an immature animal with 7 growth layer groups and two mature animals with 10 groups.

Perrin et al. (1977) found a mean length at sexual maturity of about 175-180 cm (the middle of several estimates based on different criteria, and the estimate which is most comparable with that applied to the present sample) and a mean age at sexual maturity of about 10-12 groups in the eastern spinner dolphin. As was seen when comparing the sexual maturity figures for females from the two populations, the eastern spinner reaches maturity at a shorter length than our sample from the Gulf of Mexico. In the case of males, the ages at attainment of sexual maturity are more similar and the length difference is probably due to population differences in mean size of individuals.

PRODUCTIVE SEASONALITY

Of the six mature females in this sample, one (504456) was lactating and one had a large corpus luteum with no visible conceptus. Both of these had probably given birth recently. None of the six were pregnant. Six of the seven mature males were examined for presence of sperm in the epididymis. Sperm was present in all six and was judged to be copious in three. Admittedly, this is a very small sample, but it is indicative of recent calving and breeding activity.

Perhaps the most convincing evidence for recent reproductive activity in this sample are the three calves which were present, with lengths of 90, 91, and 97 cm. Perrin et al. (1977) estimated length at birth in the eastern spinner to be 75.5 cm. Since the mean lengths of mature animals and the mean lengths at attainment of sexual maturity in the Florida sample are uniformly about 14% greater than the corresponding figures for the eastern spinner dolphin, it is logical to assume, for an initial approximation, that length at birth would also be about 14% greater, or about 86 cm. Perrin et al. (1977) estimated the postnatal growth rate in the first 10 or 11 mo after birth to be 4.77 cm/mo. Again, allowing a difference of 14% for the larger mean size in the Florida sample, a usable estimate of the growth rate during this period would be 5.4 cm/mo. This provides projected ages for the two smaller calves of about 1 mo old, and for the larger of about 2 mo, with birth dates of mid-June and mid-May.

The only other data available for spinner dolphins in the Gulf of Mexico are the 8.1 cm fetus which Layne (1965) found in an animal which stranded in mid-September and the 61 cm fetus which Schmidley and Shane (see footnote 5) found in early March. Using the fetal growth curve for the eastern spinner (Perrin et al. 1977), and assuming that the mean size difference between the populations would not be significant for small fetuses, the approximate date of conception for the

8.1 cm fetus would be late June or early July, and for the 61 cm fetus would be early May.

Thus, although the data are few, there is a convincing consistency indicative of a calving season for this population in early summer (May-July).

PHYSICAL MATURITY

Physical maturity was judged on the basis of examination of the epiphyseal suture in one of the midthoracic vertebrae and noting whether a cartilaginous plate was present (open), absent but with the epiphyseal line still visible (closed), or absent with all trace of the epiphyseal suture obliterated (fused). The suture was examined on a cut surface at least 1 cm deep, and generally on a median section of a whole centrum. Closure of the suture takes place last along the periphery of the epiphyseal plate, and a shallow cut can frequently be misleading. As can be seen in Table 2, males reached physical maturity at about the same size as sexual maturity (with the exception of 504447, which as noted earlier, was probably an abnormal individual). Females, however, reached physical maturity considerably after sexual maturity, at a length of about 196 cm and a weight of about 61 kg.

EXTERNAL MORPHOLOGY

External measurements were taken in the manner outlined by Norris (1961), at the time the animals were picked up from the beach, using a steel tape graduated in centimeters. Numbers in parentheses in the text refer to the numbered measurements as defined in that paper. In the following discussion, relative dimensions are with respect to the total length of the individual, and are expressed as the means of the individual dimensions divided by the individual total lengths (Table 3). Figure 2 shows the long slender rostrum and a pigmentation pattern characteristic of this species.

Sexual dimorphism in the external measurements was most apparent in the relative length of the rostrum (snout to apex of melon (3)). This dimension was about 7% larger in females for the total sample, but was less in the adult and neonatal samples. Perrin (1975) found the same sexual difference in the sample of *S. longirostris* which he examined from the Pacific.

The other anterior body measurements which are taken from the tip of the snout show sexual differences of a lower relative magnitude, due to inclusion of the rostral length as a component of these dimensions. We should then expect, if no other factors were active, that all measurements containing rostral length would be proportionately greater in females, and all those not containing rostral length would be proportionately smaller. In this particular sample, however, the variation is such that these differences are not apparent in most cases.

TABLE 3.—External measurements on Florida spinner dolphin expressed as individual dimensions divided by individual total lengths. For these purposes animals with a total length >195 cm were considered adult. Numbers in parentheses refer to Norris (1961) for definitions of the measurement.

Measurement	Sample	*N*	Mean	SD
Snout to apex of melon (3)	Total males	12	0.089	0.005
	Total females	14	.095	.008
	Adult Males	9	.090	.005
	Adult females	4	.093	.005
	Neonatal males	1	.080	—
	Neonatal females	2	.081	.005
Snout to genital slit (13)	Adult males	9	.652	.020
	Adult females	5	.706	.023
Girth at anus (23)	Adult males	9	.312	.012
	Adult females	5	.281	.022
Fluke width (34)	Total males	12	.233	.017
	Total females	15	.216	.017
	Adult males	9	.235	.019
	Adult females	5	.222	.016
	Neonatal males	1	.221	—
	Neonatal females	2	.210	.014
Height of dorsal fin (32)	Total males	12	.102	.009
	Total females	15	.095	.006

The position of the center of the genital slit, as determined by the measurement from the tip of the snout to the genital slit (13), differs between males and females, with the center of the slit being farther posterior in females. The difference amounts to a relative increase of about 8% in this measurement in adult females when compared with adult males. This particular sexual difference seems to be true of cetaceans in general.

Girth at the anus (23) relative to total length is about 11% greater in adult males. This is correlated with development of a postanal keel in adult males as described by Perrin (1972, 1975).

The relative width of the flukes (34) was 5-8% greater in males in the adult, total, and neonatal samples. Although the variation in this character renders this statistically insignificant in this sample, the same sort of difference was found by Perrin (1975) in his Pacific samples, suggesting that it is a real difference. The relative height of the dorsal fin (32) was 7% greater in males in the total sample. Here again, the variation renders the difference statistically insignificant. There is a possible indication that the flippers are relatively larger in females, but the difference is slight

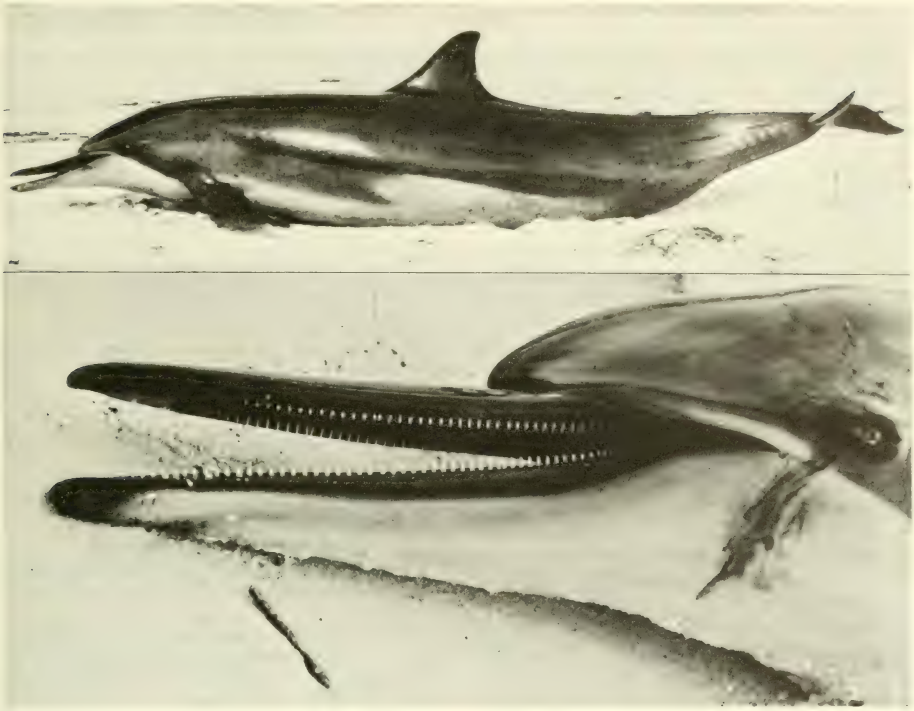


FIGURE 2.—Adult *Stenella longirostris* stranded at Casey Key, Fla. Above adult male, 195 cm total length (504442); below, head of adult female, 186 cm total length (504454).

enough that a larger sample would be needed to demonstrate its validity.

None of the other measurements show any appreciable sexual differences when the differences in total length and rostral length are taken into account.

Since the sample is lacking in intermediate-size animals, there is relatively little that can be said about growth patterns. It is apparent that the snout is relatively shorter and the rest of the head relatively larger in neonatal animals than in adults. The girths appear to be relatively greater, the flippers relatively larger, but the flukes and dorsal fin about the same proportion in the neonates as in the adults. Although the sample of neonates is too small to have any statistical significance, the sexual differences in length of rostrum, position of genital slit, width of flukes, and height of dorsal fin are the same in the neonates as in the adults.

Although comparable data for samples of *S. longirostris* from other areas are sparse (Perrin 1975), this sample appears to be similar to Hawaiian spinners in total length, rostral length, and girths. More meaningful comparison to other populations of *S. longirostris* will require increased sample sizes and more sophisticated statistical procedures.

WEIGHTS

The body weights of 11 males (188-208 cm) ranged from 51 to 75 kg, with a mean of 63.8 kg, while the body weights of 13 females (177-204 cm) ranged from 46.1 to 65.2 kg, with a mean of 55.7 kg. Thus, while the sample of males averaged about 3% longer than the sample of females, they averaged about 14% heavier. The range of individual organ weights and the mean percentages of total body weight are as follows, with the comparable data for Pacific spinner dolphins given by Perrin and Roberts (1972) in parentheses; heart 260-440 g, 0.59% (191-272 g, 0.46%); liver 980-2,200 g, 2.7% (832-997 g, 1.90%); kidneys 350-620 g, 0.78% (289-393 g, 0.65%); brain 500-780 g, 1.02%. The organ weights in the Florida sample, expressed as mean percentage of body weight, averaged about 25% greater than those given for the Pacific spinner dolphins. It is possible that some of this difference is due to weight loss (primarily blubber and muscle) in the Florida sample induced by the stress of whatever factors led to their stranding. As noted earlier, the stomachs of all of the Florida specimens were empty, and it is likely that they had not fed for some time. Perrin and Roberts (1972) noted that in both their samples of spotted and spinner dolphins, the right kidneys tended to be larger than the left whereas in our sample the kidneys were essentially equal (left was heavier in nine, right was heavier in five, and both were equal in eight).

ACKNOWLEDGMENTS

The authors particularly wish to acknowledge the help of Perry Gilbert and the staff of the Mote Marine Laboratory, who provided facilities and assistance in the necropsy. We also wish to thank Edward Asper and the staff of Sea World, Inc., Orlando, for data on the two live animals which were transported to their facilities. Vladimir Gurevich of the Hubbs-Sea World Research Institute, San Diego, and J. E. Reynolds of the University of Miami assisted in the necropsies and in the preparation of skeletal material. William F. Perrin, Southwest Fisheries Center, NMFS, NOAA, La Jolla, kindly read the manuscript and provided criticism and suggestions.

LITERATURE CITED

CALDWELL, D. K., M. C. CALDWELL, W. F. RATHJEN, AND J. R. SULLIVAN.
1971. Cetaceans from the Lesser Antillean island of St. Vincent. Fish. Bull., U.S. 69:303-312.

ERDMAN, D. S., J. HARMS, AND M. M. FLORES.
1973. Cetacean records from the northeastern Caribbean region. Cetology 17, 14 p.

GERACI, J. R.
1978. The enigma of marine mammal strandings. Oceanus 21(2):38-47.

GUNTER, G.
1954. Mammals of the Gulf of Mexico. *In* P. Galtsoff (editor), Gulf of Mexico, its origin, waters, and marine life, p. 543-551. U.S. Fish Wildl. Serv., Fish. Bull. 55.

HARRISON, R. J., R. L. BROWNELL, JR., AND R. C. BOICE.
1972, Reproduction and gonadal appearances in some odontocetes. *In* R. J. Harrison (editor), Functional anatomy of marine mammals, Vol. 1, p. 361-429. Acad. Press, N.Y.

LAYNE, J. N.
1965. Observations on marine mammals in Florida waters. Bull. Fla. State Mus. 9(4):131-181.

LOWERY, G. H.
1974. The mammals of Louisiana and adjacent water. La. State Univ. Press, Baton Rouge, 565 p.

NORRIS, K. S.
1961. Standardized methods for measuring and recording data on the smaller cetaceans. J. Mammal. 42:471-476.

PERRIN, W. F.
1972. Color patterns of spinner porpoises (*Stenella* cf. *S. longirostris*) of the eastern Pacific and Hawaii, with comments on delphinid pigmentation. Fish. Bull., U.S. 70:983-1003.
1975. Variation of spotted and spinner porpoises (genus Stenella) in the eastern Pacific and Hawaii. Bull. Scripps Inst. Oceanogr. 21, 206 p.

PERRIN, W. F., J. M. COE, AND J. R. ZWEIFEL.
1976. Growth and reproduction of the spotted porpoise, *Stenella attenuata*, in the offshore eastern tropical Pacific. Fish. Bull., U.S. 74:229-269.

PERRIN, W. F., D. B. HOLTS, AND R. B. MILLER.
1977. Growth and reproduction of the eastern spinner dolphin, a geographical form of *Stenella longirostris* in the eastern tropical Pacific. Fish. Bull., U.S. 75:725-750.

PERRIN, W. F., AND E. L. ROBERTS.
1972. Organ weights of non-captive porpoise (*Stenella* spp.). Bull. South. Calif. Acad. Sci. 71:19-32.

SHANE, S. H.
1977. The population biology of the Atlantic bottlenose dolphin, *Tursiops truncatus*, in the Aransas Pass area of Texas. M.S. Thesis, Texas A&M Univ., College Station, 239 p.

TARUSKI, A. G., AND H. E. WINN.
1976. Winter sightings of odontocetes in the West Indies. Cetology 22, 12 p.

ANNUAL VARIABILITY OF REEF-FISH ASSEMBLAGES IN KELP FORESTS OFF SANTA BARBARA, CALIFORNIA

ALFRED W. EBELING,[1] RALPH J. LARSON,[2] WILLIAM S. ALEVIZON,[3] AND RICHARD N. BRAY[4]

ABSTRACT

Assemblages of kelp-bed fishes that live in and about the kelp canopy or over the reef bottom were censused by movie strips (cinetransects) every September from 1971 to 1974 at rock reefs off Santa Barbara, southern California. Cinetransects provided an adequate and efficient way to estimate species composition (order of relative or ranked species abundances), diversity, and numbers of fish for yearly comparisons between canopy and bottom habitats at mainland and Santa Cruz Island study sites. Canopy assemblages were simpler and more variable than bottom assemblages. They differed less in composition between sites. Between-site differences in fish assemblages reflected differences in structural habitat between mainland and island. Variation in species composition was less among years than between habitats or sites in the sense that site- and habitat-specific composition of assemblages persisted in the course of significant yearly changes in counts of fish and species per transect. Despite these changes, "annual variation," as measured by variance of year-to-year $\log_{10}$ ratios of numbers of 16 common species, was relatively small. Its size was characteristic of stable communities in predictable environments. As a group, planktivores, which form dense aggregations in midwater, fluctuated most in numbers. Perhaps fish responded directly to local changes in water clarity, temperature, currents, and density of giant kelp. However, coincident changes in fish counts at mainland and island sites indicated that these local environmental factors, which did not vary accordingly, were not the only causes of annual variability in fish abundance.

Off southern California, rocky reefs and beds of giant kelp, *Macrocystis pyrifera*, harbor more than 125 species of fish, almost 25% of the Californian marine total (Quast 1968b; Feder et al. 1974). Subtidal reef-fish assemblages have been extensively studied in the warm-temperate San Diegan Faunal Region to the south of Santa Barbara (Quast 1968b, c; Hobson and Chess 1976; Limbaugh[5]), and in the cool-temperate Montereyan Faunal Region to the north (Miller and Geibel 1973; Burge and Schultz[6]; Gotshall et al.[7]). Except for scattered observations and species lists (Hewatt 1946; Quast 1968c; Clarke and Neushul 1967; Neushul et al. 1967; Alevizon 1976), however, virtually nothing is known of the structure and annual variability of such fish assemblages off Santa Barbara, which is at the northern end of the San Diegan Region as defined by Hubbs (1960).

Ebeling et al. (in press) analyzed Santa Barbaran assemblages of kelp-bed fishes sampled from a variety of habitats and localities along the mainland coast and across the Santa Barbara Channel at Santa Cruz Island. The fish community was assumed to comprise smaller groups of species that tend to segregate among habitat types. Photographic observations made throughout 1970 were used to resolve five such "habitat groups." A group of "kelp-rock species" (e.g., garibaldi, *Hypsypops rubicundus*, and California sheephead, *Pimelometopon pulchrum*) was most abundant in relatively clear water and dense kelp over high-relief rocky reef. "Canopy species" (e.g., kelp

[1]Department of Biological Sciences and Marine Science Institute, University of California, Santa Barbara, CA 93106.

[2]Department of Biological Sciences and Marine Science Institute, University of California, Santa Barbara, Calif.; present address: MRC Research Center, 533 Stevens Ave., Solana Beach, CA 92075.

[3]Department of Biological Sciences and Marine Science Institute, University of California, Santa Barbara, Calif.; present address: Department of Biological Sciences, Florida Institute of Technology, Melbourne, FL 32901.

[4]Department of Biological Sciences and Marine Science Institute, University of California, Santa Barbara, Calif.; present address: Department of Biology, California State University, Long Beach, CA 90840.

[5]Limbaugh, C. 1955. Fish life in the kelp beds and the effects of kelp harvesting. Univ. Calif. Inst. Mar. Resour., IMR Ref. 55-9, 158 p.

[6]Burge, R. T., and S. A. Schultz. 1973. The marine environment in the vicinity of Diablo Cove with special reference to abalones and bony fishes. Calif. Dep. Fish Game Mar. Resour. Tech. Rep. 19, 433 p.

[7]Gotshall, D. W., L. L. Laurent, E. E. Ebert, F. E. Wendell, and G. D. Farrens. 1974. Diablo Canyon power plant site ecological study annual report July 1, 1973—June 30, 1974. *In* W. J. North (editor), Environmental investigations at Diablo Canyon, 1974. Calif. Dep. Fish Game Mar. Resour. Admin. Rep. 74-10, p. 199-305.

Manuscript accepted October 1979.
FISHERY BULLETIN: VOL. 78, NO. 2, 1980.

perch, *Brachyistius frenatus*, and señorita, *Oxyjulis californica*) usually aggregated within and just below the kelp canopy; "bottom species" (e.g., gopher rockfish, *Sebastes carnatus*) rested on the rocky reef surface far below; while "commuter species" (e.g., kelp bass, *Paralabrax clathratus*) swam about at all depths. "Inner-marginal species" (e.g., black perch, *Embiotoca jacksoni*) occurred abundantly over mixed rock and sand inshore as well as deeper reefs offshore. Members of different groups tended to mingle in areas of continuous reef and kelp where habitat types were close together. The more complex and extensive island reefs harbored the greatest numbers of "reef specialists" in the kelp-rock group.

The present study is an analysis of annual variability in species composition, diversity, and abundance of kelp-bed fishes in the faunistically transitional (Neushul et al. 1967; Hubbs 1974; Horn and Allen 1978) Santa Barbara Channel. There have been few long-term studies of stability and variability in reef-fish communities (Thomson and Lehner 1976; Sale 1978). Yet, understanding the scope and causes of variation in natural communities has both practical and theoretical importance (Larkin 1978; Wolda 1978). Our primary purposes, therefore, were to 1) document yearly changes in kelp-bed fish assemblages, which had previously impressed us as appearing relatively uniform in time, and 2) relate observed changes to environmental variables that we could readily observe. Secondarily, we assessed the use of underwater movies to census fishes in a complex environment. To these ends, we made annual censuses of fishes in and about the canopy of giant kelp and over the bottom in areas of continuous rock reef at sites off the Santa Barbara mainland and Santa Cruz Island.

METHODS

Study Sites

Sampling was conducted in areas of rocky reef and kelp on either side of the Santa Barbara Channel (Figure 1). Our mainland sampling site was Naples Reef, an isolated system of rocky outcrops and ledges located about 1.6 km offshore, 24

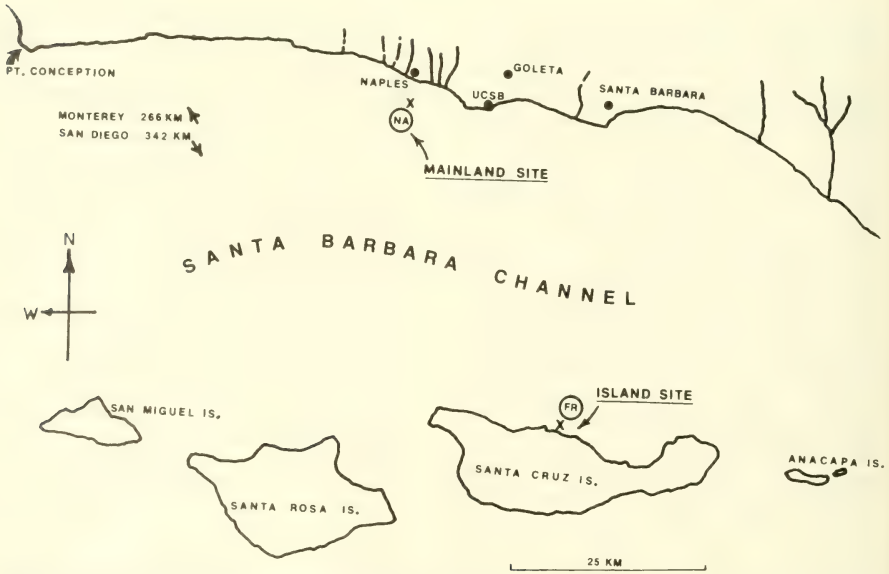


FIGURE 1.—Study sites for yearly sampling of fish assemblages in areas of reef and kelp off Santa Barbara, southern California. Circled letters identify the mainland site, Naples Reef (NA), and the island site, Fry's Harbor and vicinity (FR).

km west of Santa Barbara, Calif. (lat. 34°25′ N, long. 119°57′ W). Measuring 275 × 80 m (2.2 ha), the reef surface averaged 8-12 m in depth, though some crests projected to within 5 m of the surface. The reef was surrounded by flat sand or cobble bottom, 16-20 m deep, with smaller rock outcrops. Above the reef, the kelp canopy usually proliferated during spring and summer, but thinned during late fall and winter.

Island observations were made at a site centered about Fry's Harbor on the north side of Santa Cruz Island (Figure 1). The subtidal substrates here were mostly rocky, with boulder areas, ledges, and caves interspersed occasionally with sand or flat-faced rock. The bottom sloped rather steeply to sand at depths of 15-25 m about 20-50 m from shore. Most sampling was conducted at depths of 3-15 m. Here, the kelp canopy extended a short distance seaward over greater depths and shoreward to meet steep rock cliffs. In contrast with the mainland observations, therefore, most island observations were made within about 10-50 m of the shore, over an area of rapidly increasing bottom depth.

We saw anglers and divers at both sites. Yet, we rarely observed concentrated fishing effort, probably because of the erratic state of the Santa Barbara partyboat industry during the early 1970's (Love and Ebeling 1978). Fishermen in small boats were more frequently seen casting bait and lures near the surface at Naples Reef than at the island site. Hence, catches of kelp bass and other surface predators were probably substantial at Naples Reef only. Sport divers exploited both sites, albeit more sporadically than boat fishermen and seldom during the sampling periods. We suspect that catches of bottom fishes were not large and about the same at both sites.

We noted no kelp cutting and harvesting in the area of either site. About the island site, kelp beds are limited to a narrow band along the steep shore, and so are inaccessible and too small for harvest.[8] Kelp in the mainland area is harvested only inshore of Naples Reef, which is left undisturbed.[9]

Cinetransects

We sampled fish and observed habitat characteristics by means of "cinetransects." These were 2.5-min, Super-8 mm[10] movie films taken at 24 frames/s by scuba divers. The use of 50 ft (15.24 m) film cartridges standardized sampling time, and allowed rapid changing of film. High-speed color film yielded good photographs when water visibility exceeded 3 m. Starting from opportune points within the kelp-rock habitat, divers swam at relatively constant speeds, and, with the camera held level or pointed slightly downward (for bottom transects), steadily panned in about 10° arcs. Large aggregations of fish were photographed in one sweep of the camera; thereafter the camera was not pointed at the aggregation. This procedure allowed rapid and accurate enumeration of aggregations, and avoided redundant sampling of fish. During a given transect, a diver would keep to the same general depth and terrain, so that each transect could be classified by its habitat characteristics. For each transect, he measured depth of filming, depth of bottom, underwater visibility, temperature, and depth of thermocline. Films were taken in two general habitats: bottom and kelp canopy. Canopy transects were made at depths of 2-3 m, just below the mat of floating fronds. Bottom transects were taken from about a meter above the bottom, at depths ranging from about 3 to 15 m. All cinetransects were photographed during September of the years 1971-74. This was in the midst of the season of maximum thermal stratification, when water was predictably calm and clear (Brown 1974; Love and Ebeling 1978).

Two observers counted and tallied individuals per species from cinetransects projected at low speed and stop action. For each film, observers also scored bottom relief and algal density from 1 (low) to 5 (high). They often stopped, reversed, and reran the film to accurately count fish in dense clusters. When observers disagreed, they recounted, and recorded the average of the two closest values. All species but two were tallied separately. The sibling rockfishes *Sebastes carnatus* and *S. chrysomelas*, which were identifiable by color only, were tallied as one, because subtle color differences were not always discernible in cinetransects filmed at greater depths or in more turbid water. Observers did not count small (young-of-year) juveniles, such as the reddish growth stage of blue rockfish, *S. mystinus*. Nor did

[8]Ron H. McPeak, Senior Marine Biologist, Kelco Corp., 2145 East Belt St., San Diego, CA 92113, pers. commun. October 1979.

[9]Bruce W. W. Harger, General Manager, Neushul Mariculture Corp., 275 Orange St., Goleta, CA 93017, pers. commun. October 1979.

[10]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

they count island seaperch, *Cymatogaster gracilis*, in 1971-73 samples. Island seaperch were observed only at Santa Cruz Island, sporadically in dense schools in the kelp canopy. To judge the effect of ignoring this species in 1971-73, we compared two 1974 samples, one with, the other without counts of island seaperch.

Bottom cinetransects were calibrated for area covered by estimating their length and width in the field. We estimated length experimentally by measuring distances swam during transects at Naples Reef. On each of five weekly tests, one diver photographed while a second followed with a tape measure. On 4 of 5 days, one transect went upcurrent, the other downcurrent; on the fifth day, three transects were measured in almost no current. Lengths of all 11 transects averaged 47.8±2.78 m (95% confidence interval—CI). We estimated transect width by counting markers placed along a surveyed course. A tape measure marked the midline of a 50 m stretch of reef flat and rill, and pairs of red floats, anchored 2 m on either side of the tape at 5 m intervals, delimited a 4 m wide band. Four transects were photographed along the course, with divers panning the camera as usual. While viewing the projected films, we estimated widths of pans by taking 4 m (width of the marked band) and adding or subtracting estimated distances before or beyond each float seen at the extremes of the pans. Since widths of 43 pans averaged 4.41±0.288 m (95% CI), the area covered by an average bottom transect was taken as 47.8 m (length) times 4.41 m (width) = 211 m².

Calibration of canopy transects was inherently less accurate. Photographers swam more circuitous routes at more variable speeds in midwater, where light fluctuated between dim and bright. The best we could do was roughly measure distance travelled by a photographer swimming unidirectionally under the canopy: an average length of 62.3 m in four trials both with and against the current. We estimated band width by counting kelp blades (which averaged 0.5 m long) passed during sweeps of the camera: counts usually varied from 8 to 10, translating to 4-5 m. Hence, we assumed band width of canopy transects to equal that for bottom transects (4.41 m), and estimated area covered by a canopy transect as 62.3 m (length) times 4.41 m (width) = 275 m².

Statistical Analyses

Samples were specific for habitat, site, and year. For example, one sample was made up of fish counts from a set of 43 transects filmed in the canopy habitat at the mainland site during 1974.

Sample species diversity of yearly canopy or bottom samples of fish assemblages in mainland and island sites was measured by information-theoretical indices (H), combining species "richness" (total species) and "evenness" (distribution of individuals among species). We used Pielou's (1966) method to estimate population diversity from a set of cinetransects pooled incrementally in random order. Diversity (Brillouin's H) of successively larger subsamples (size k) first increases and then levels off, as the decrease in diversity from adding more individuals of common species balances the increase from adding rare species. Then increments of diversity per added individual (h_k) between adjacent subsample estimates (H_{k-1} and H_k) are independent, and the mean ($\bar{h}$) and variance of h_k's estimate the corresponding population parameters. Species richness (S) was the species count in a whole sample of size $k = n$. Species evenness (J) was the ratio $H_n/\ln S$, where H_n is sample diversity and $\ln S$ (natural log of species count) is the theoretically maximum value of H_n if the S species were equally abundant.

We compared species composition between sites and among years by proportionate similarity and rank correlation. Similarity (I) in species composition was measured as: $I = 1.0 - [0.5(\sum_{i=1}^{S} |p_{ij} - p_{ik}|)]$, where p_{ij} is the proportionate abundance of species i in sample j. Rank correlation (Kendall's tau) was measured between ranked species arrays (Johnson and Koo 1975). Clusters of similar samples were computed from matrices of I by the unweighted pair-group method using arithmetic averages (Sneath and Sokal 1973).

Mean counts of individuals and species per transect were compared between sites and among years (1971-74) by two-way analysis of variance (ANOVA) for unequal and disproportionate subclass sizes, and by one-way ANOVA for unequal sample sizes (Nie et al. 1975; Meeter and Livingston 1978). With variates transformed, sample distributions tended to normality (as indicated by nonsignificant Kolmogorov-Smirnov tests of goodness-of-fit) and sample variances equalized (as indicated by nonsignificant F_{max} tests of largest variance ratios) (Sokal and Rohlf 1969; Meeter and Livingston 1978). A posteriori contrasts among means were obtained by grouping means with nonsignificant ranges (Dunnett 1970; Nie et al. 1975).

Annual variability (AV) in numbers of fish per species was measured as variance in $\log_{10}$ ratios ($\log R$) of estimated numbers per hectare between consecutive years. For each species, we estimated number per hectare by summing mean counts per bottom and canopy cinetransects after correcting canopy means for greater area covered per transect, then multiplying by 47.39, the estimated number of bottom transects covering 1 ha (which approximates the average number per year, 44.12). According to Wolda (1978), $\log R = \log N_i - \log (N_{i-1})$, where N_i is number of individuals for 1 yr and N_{i-1} is that for the preceding year. The mean $\log R$ for an array of species indicates the average net change in species abundance, and the variance of the $\log R$'s (AV) measures the scope of change in species abundances. For example, a mean $\log R$ near zero indicates that about as many species increased as decreased in abundance between years, while a relatively low AV shows that increases and/or decreases were generally small; i.e., that annual variability was low. To increase the reliability of R, only species with at least 5 individuals/ha per year were included in the analysis (Wolda 1978). Although samples covered more than 2 yr, arrays must appear in calculations only once (Wolda 1978). Thus, we computed AV's for an array of 16 $\log R$'s for ratios of species abundances between 1972 and 1971, and for a similar array between 1974 and 1973 (separately for mainland and island study sites). Then, we computed overall AV between the years from the array of 32 $\log R$'s: those for 1972-71 plus those for 1974-73.

RESULTS

Yearly sampling yielded 297 and 331 cinetransects from mainland and island study sites, and recorded 46 fish species in 21 families, although only 31 species in 11 families were common enough to be analyzed (Table 1).[11] On the average, about 35 transects were needed to record 90% of 16 species that were filmed in the kelp-canopy habitat (the "canopy assemblage" of fishes), while 50 transects were needed to record 90% of 31 species that were filmed in the reef-bottom habitat (the "bottom assemblage").

Although our primary objective was to measure yearly variability, our analysis revealed significant differences in species composition, diversity, and abundance of fish assemblages between canopy and bottom habitats, and between mainland and island study sites. Therefore, we describe the observed spatial differences as a prelude to the account of yearly differences.

Spatial Differences

Differences in composition between assemblages in canopy and bottom habitats were obvious and easily demonstrated. For example, canopy and bottom arrays from all years and both sites were segregated in the cluster analysis based on proportionate species abundances (Figure 2). Canopy samples contained relatively more planktivores and kelp browsers like blacksmith, *Chromis punctipinnis*; kelp perch; blue rockfish; juvenile olive rockfish, *S. serranoides*; and señorita (Table 1). Bottom samples contained more bottom grazers and ambushers like pile perch, *Damalichthys vacca*; black perch; garibaldi; California sheephead; gopher rockfish; and black-and-yellow rockfish, *S. chrysomelas*.

The canopy assemblage was simpler than the bottom assemblage in the sense that more individuals of fewer species occurred in the canopy. All of our 31 common species were recorded in bottom cinetransects, but only 16 were filmed in the canopy (Table 1). Furthermore, while the median number of individuals (33—corrected for greater volume per transect) recorded in canopy transects significantly exceeded that (24) for bottom transects, the median species count (5) was significantly less than that (8) in bottom transects (Wilcoxon tests based on 275 canopy and 353 bottom counts, $P<0.005$). These differences were reflected in the shapes of the abundance-diversity curves for the two habitats (Figure 3). Those from the canopy habitats sloped steeply, reflecting the fact that only a few species were relatively common there, while those from the bottom habitats had flatter tops, reflecting a more coequal commonness of several species.

In general, the composition of fish assemblages differed markedly between mainland and island

[11] Additional species that were rarely recorded include: *Heterodontus francisci* (Heterodontidae), *Cephaloscyllium ventriosum* (Scyliorhinidae), *Myliobatis californica* (Myliobatididae), *Torpedo californica* (Torpedinidae), *Syngnathus* spp. (Syngnathidae), *Atherinops affinis* (Atherinidae), *Cymatogaster gracilis* (Embiotocidae—sporadically common at island, see text), *Phanerodon atripes* (Embiotocidae), *Caulolatilus princeps* (Branchiostegidae), *Gibbonsia elegans* (Clinidae), *Coryphopterus nicholsi* (Gobiidae), *Scorpaena guttata* (Scorpaenidae), *Sebastes auriculatus* (Scorpaenidae), *Pleuronichthys coenosus* (Pleuronectidae), and *Mola mola* (Molidae).

TABLE 1.—Relative abundance of 31 species of kelp-bed fishes from canopy and bottom assemblages in yearly cinetransect samples filmed during 1971-74 at mainland and Santa Cruz Island study sites off Santa Barbara, southern California (Figure 1). Values are percent number of individuals.

	Kelp canopy habitat										Reef bottom habitat									
	Santa Barbara mainland					Santa Cruz Island					Santa Barbara mainland					Santa Cruz Island				
Family and species	1971	1972	1973	1974	1971-74	1971	1972	1973	1974	1971-74	1971	1972	1973	1974	1971-74	1971	1972	1973	1974	1971-74
Serranidae																				
Paralabrax clathratus	9.96	2.87	6.85	2.51	4.56	1.39	3.12	5.47	4.70	3.34	20.78	12.48	6.30	7.01	10.86	9.92	13.39	21.20	10.88	13.82
P. nebulifer	—	—	—	—	—	—	—	—	—	—	0.17	0.05	—	—	0.04	—	—	—	—	—
Sciaenidae																				
Cheilotrema saturnum	—	—	—	—	—	—	—	—	—	—	—	0.09	0.10	1.45	0.53	—	—	—	—	—
Kyphosidae																				
Girella nigricans	12.45	—	—	1.11	1.12	1.19	4.21	0.59	3.43	2.72	2.04	10.79	5.92	3.50	7.00	18.39	8.24	10.95	8.46	11.27
Medialuna californiensis	6.51	3.27	1.86	5.09	3.42	0.08	0.26	0.46	0.46	0.28	0.17	0.70	0.67	7.01	2.12	1.13	0.59	0.70	1.40	0.94
Embiotocidae																				
Brachyistius frenatus	—	—	7.30	0.22	2.28	52.99	37.07	24.70	11.79	34.60	—	—	0.29	0.08	0.08	1.05	1.58	0.16	0.37	0.81
Damalichthys vacca	0.19	0.03	—	0.15	0.06	0.16	0.08	0.13	0.06	0.10	9.03	4.77	6.69	4.70	5.66	2.58	4.22	4.12	2.87	3.48
Embiotoca jacksoni	—	0.07	—	0.44	0.11	—	—	0.13	0.58	0.13	23.34	22.62	43.55	25.90	27.91	8.63	7.92	7.22	6.84	7.64
E. lateralis	—	0.23	—	0.66	0.22	0.04	0.31	2.50	0.70	0.66	2.56	6.45	3.92	1.88	4.37	2.18	3.10	4.35	1.84	2.87
Hypsurus caryi	—	—	—	—	—	—	—	—	—	—	2.39	2.94	7.74	17.95	7.65	—	0.46	0.08	—	0.15
Phanerodon furcatus	2.68	—	2.81	0.44	1.15	—	—	0.33	0.58	0.16	0.17	0.75	2.20	0.51	0.93	0.32	0.59	0.31	0.81	0.52
Rhacochilus toxotes	0.19	—	0.04	—	0.03	0.04	—	—	—	0.01	5.96	1.92	1.62	0.77	2.04	0.16	1.91	1.24	1.18	1.17
Pomacentridae																				
Chromis punctipinnis	51.92	29.00	37.48	42.03	35.79	39.72	35.46	11.13	39.95	33.49	9.03	7.71	2.20	10.68	7.44	16.69	7.26	0.54	25.88	12.51
Hypsypops rubicundus	—	—	—	—	—	—	—	—	—	—	—	1.26	0.76	1.45	1.05	13.14	17.08	10.87	12.35	13.51
Labridae																				
Halichoeres semicinctus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.32	0.33	0.16	0.29	0.28
Oxyjulis californica	4.60	3.76	15.02	10.03	8.51	1.11	3.98	8.96	11.61	5.42	8.52	8.97	2.67	5.47	6.76	1.69	2.38	3.18	5.81	3.28
Pimelometopon pulchrum	—	0.03	0.04	—	0.03	—	0.05	—	0.06	0.03	2.22	4.16	2.10	1.11	2.77	13.39	11.68	9.86	8.31	10.79
Clinidae																				
Heterostichus rostratus	0.19	0.07	0.27	0.30	0.18	0.08	0.03	0.07	—	0.04	—	0.09	0.76	0.94	0.42	—	0.13	—	0.15	0.07
Scorpaenidae																				
Sebastes atrovirens	0.38	0.30	0.50	0.22	0.35	1.39	2.62	3.49	8.30	3.47	0.51	0.28	0.67	0.59	0.47	6.05	8.31	7.38	5.52	6.88
S. carnatus & S. chrysomelas	—	—	—	—	—	—	—	—	—	—	2.22	0.75	3.25	2.39	2.00	0.56	2.31	2.48	0.88	1.59
S. melanops	—	—	—	—	—	—	—	—	—	—	—	—	0.19	—	0.04	—	—	—	—	—
S. mystinus	10.92	59.81	27.49	35.18	41.26	0.04	10.63	3.82	9.76	6.67	7.16	11.03	4.20	2.74	7.12	0.56	5.08	11.57	3.68	5.24
S. rastrelliger	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.56	0.53	0.47	0.22	0.44
S. serranoides	—	0.56	0.36	1.62	1.67	1.72	2.18	38.21	8.01	8.85	1.02	0.28	0.10	0.68	0.42	1.05	1.38	1.94	1.47	1.46
S. serriceps	—	—	—	—	—	—	—	—	—	—	0.17	—	0.10	—	0.04	0.16	0.20	0.08	0.22	0.18
S. vexillaris	—	—	—	—	—	—	—	—	—	—	0.17	0.09	—	—	0.06	—	—	0.08	—	0.02
Hexagrammidae																				
Ophiodon elongatus	—	—	—	—	—	—	—	—	—	—	—	0.05	0.38	—	0.10	—	—	—	—	—
Oxylebius pictus	—	—	—	—	—	—	—	—	—	—	2.39	1.68	3.25	2.91	2.39	1.45	1.12	0.85	0.59	1.00
Cottidae																				
Leiocottus hirundo	—	—	—	—	—	—	—	—	—	—	—	—	0.10	—	0.02	—	—	0.08	—	0.02
Scorpaenichthys marmoratus	—	—	—	—	—	—	—	—	—	—	—	0.05	0.29	0.26	0.14	—	0.20	0.16	—	0.09
Number of individuals	522	3,031	2,204	1,356	7,113	2,442	3,847	1,518	1,722	9,529	587	2,140	1,047	1,170	4,944	1,240	1,516	1,288	1,360	5,404
Number of cinetransects	13	31	45	40	129	22	38	46	40	146	25	45	55	43	168	37	45	55	48	185

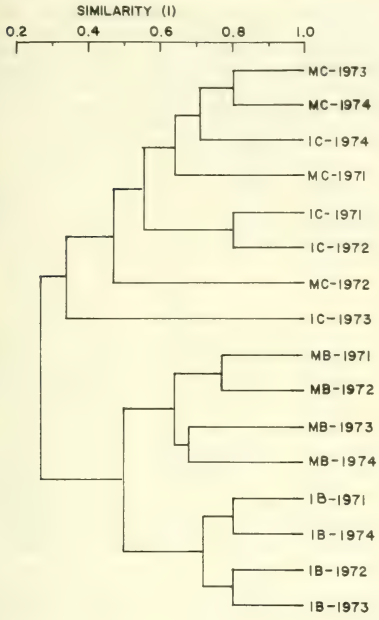


FIGURE 2.—Clustering, by year (right number), of canopy (C) and bottom (B) cinetransect samples of kelp-bed fishes filmed each September in 1971-74 at mainland (M) and Santa Cruz Island (I) study sites off Santa Barbara, southern California.

study sites. Samples from within mainland or island sites tended to be more alike than samples between these sites, particularly for bottom assemblages. Samples from within tended to form secondary subclusters nested in the principal ones distinguishing canopy and bottom assemblages (Figure 2), and within-site similarity values tended to be higher than between-site values (Table 2).

As indicated by clusters (Figure 2) and similarity values (Table 2), however, mainland and island canopy assemblages were more difficult to distinguish than bottom assemblages. The mean ratio of within- to between-site resemblance (I or tau) was comparatively large for arrays of canopy species (Table 2), indicating that canopy assemblages were only slightly more distinguishable between sites than among years. This, and the fact that variances of canopy similarities were relatively large (Table 2), explained why the clusters of canopy samples were poorly defined. What few between-site differences in canopy samples prevailed were due to greater numbers of kelp perch and juvenile olive rockfish observed in the canopy habitat of the island site, and of blue rockfish at the mainland (Table 1). Island canopy samples contained a few more species than mainland canopy samples (Table 3, S), and the average number of species per cinetransect (Table 3) was significantly greater (Table 4) at the island. (The significant year-site interaction as indicated in

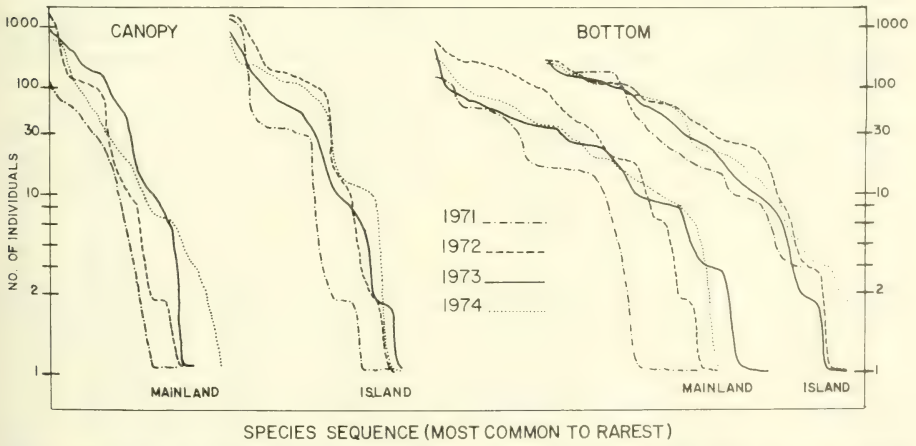


FIGURE 3.—Abundance-diversity curves for 31 species of kelp-bed fishes from canopy and bottom assemblages in yearly samples filmed during 1971-74 at mainland and Santa Cruz Island sites off Santa Barbara, southern California.

TABLE 2.—Comparison of within-site and between-site means (± 1 standard deviation) of similarity (I) and rank correlation (tau) between all pairs of species-abundance arrays from yearly cinetransect samples filmed during 1971-74 at mainland and Santa Cruz Island Study sites off Santa Barbara, southern California. Within-site means are of values for all pairs (1971 vs. 1972, 1971 vs. 1973, . . ., 1973 vs. 1974), both members of which were filmed in canopy or bottom habitats either at the mainland or island site; between-site means are of values for all such habitat-year pairs, one member of which was from an island sample, the other from a mainland sample; and mean ratio is the between-site value/mean within-site value (mainland and island). (Figure 2 is a cluster diagram of yearly samples, computed from all values of I.)

	Within sites (n = 6)[1]				Between sites (n = 10)		Mean ratio between/within	
	Mainland		Island					
Habitat	I	Tau	I	Tau	I	Tau	I	Tau
Canopy	0.62 ± 0.11	0.58 ± 0.09*	0.61 ± 0.13	0.59 ± 0.09*	0.50 ± 0.17	0.45 ± 0.12	0.81	0.77
Bottom	0.68 ± 0.05**	0.67 ± 0.06***	0.75 ± 0.06***	0.80 ± 0.03***	0.53 ± 0.09	0.49 ± 0.06	0.74	0.67
Mean	0.65	0.625	0.68	0.695	0.515	0.495	0.775	0.72

[1]Difference of within- and between-site means significant at (t-test): *P 0.05; **P 0.01; ***P 0.001

Table 4 occurred because the relation was reversed in 1973 as indicated in Table 3.) Diversity and evenness (Table 3, $\bar{h}$ and J) of canopy assemblages, however, did not differ significantly between sites.

However, sporadically abundant endemic island seaperch were not included in these comparisons. Adding this species to 1974 counts of the island-canopy samples increased the fish total from 1,722 to 3,084 individuals, median fish counts per transect from 31 to 64 individuals, and median number of species per transect from 5.5 to 6.0. The slight increase in species diversity ($\bar{h}$) was not significant (Table 3). Island seaperch were seldom observed in bottom transects.

In contrast to the canopy assemblages, mainland and island bottom assemblages were easily distinguishable. Because between-site resemblance was comparatively small for arrays of bottom species (Table 2), mainland and island clusters of samples were sharply defined (Figure 2). Island samples contained relatively more California sheephead, garibaldi, and opaleye, *Girella nigricans*, and included rock wrasse, *Halichoeres semicinctus*, which were not recorded from the mainland (Table 1). Mainland-site sam-

TABLE 3.—Yearly abundance and species diversity of canopy and bottom assemblages of kelp-bed fishes in cinetransect samples from mainland and Santa Cruz Island study sites off Santa Barbara, southern California. Columns include: n, no. of transects in sample; Geom. $\bar{x}$, the antilog of the mean transformed fish count with 95% confidence limits; S, total species in sample; $n(h)$, sample size to compute h; $\bar{h}$, the mean of successively pooled transect estimates of diversity per individual (see text); and J, evenness of distribution of individuals among species in the sample. Contrasts among means that were shown to differ significantly by analysis of variance (Table 4) were by the Student-Newman-Keuls procedure (Sokal and Rohlf 1969:239); means making up homogeneous subsets are indicated by X's in the same column.

				Fish counts			Species counts					
Habitat	Site	Year	n	Geom. $\bar{x}$, 95% CL	Contrasts		$\bar{x}$ ± 95% CI	Contrasts		S	$n(h)$	$\bar{h}$ ± 95% CI	J
Canopy	Mainland	1971	13	11.0 24.2 53.1	x	x	2.7 ± 0.63	x		11	7	1.33 ± 0.555	0.54
		1972	31	47.4 70.6 105.0		x	4.7 ± 0.57	x		12	19	1.32 ± 0.297	0.39
		1973	45	32.2 39.9 49.3	x		5.0 ± 0.42	x		12	27	1.80 ± 0.161	0.64
		1974	40	16.2 22.5 31.2	x		4.3 ± 0.57	x		14	29	1.82 ± 0.216	0.52
		Unweighted	$\bar{x}$	39.3			4.2			12.2		1.57	0.522
	Island	1971	22	30.6 58.8 112.5		x	4.6 ± 0.69	x		13	16	1.17 ± 0.187	0.40
		1972	38	51.0 70.6 97.9		x	6.2 ± 0.67		x	13	29	1.63 ± 0.137	0.61
		1973	46	19.6 25.4 32.6	x		3.5 ± 0.45	x		14	32	1.70 ± 0.301	0.58
		1974	40	21.5 29.0 39.3	x		5.7 ± 0.63		x	14	27	2.18 ± 0.199	0.71
		Unweighted	$\bar{x}$	46.0			5.0			13.5		1.67	0.575
		1974[1]	40	30.3 43.9 63.7			6.3 ± 0.71			15	29	2.32 ± 0.272	0.64
Bottom	Mainland	1971	25	15.7 20.0 25.4	x	x	7.3 ± 0.82	x	x	20	11	2.39 ± 0.167	0.75
		1972	45	36.6 42.4 48.9		x	10.1 ± 0.62		x	24	27	2.51 ± 0.130	0.76
		1973	55	13.7 16.2 19.3	x		7.0 ± 0.65	x		26	31	2.34 ± 0.185	0.68
		1974	43	18.9 22.8 27.4		x	8.2 ± 0.83		x	22	33	2.46 ± 0.116	0.77
		Unweighted	$\bar{x}$	25.4			8.2			23.0		[2]2.42	0.740
	Island	1971	37	23.6 28.6 34.6		x	8.7 ± 0.65	x	x	21	25	2.45 ± 0.107	0.77
		1972	45	24.1 28.7 34.2		x	9.5 ± 0.84		x	24	36	2.60 ± 0.089	0.82
		1973	55	16.9 19.9 23.5	x		7.8 ± 0.72	x		25	34	2.56 ± 0.123	0.78
		1974	48	17.0 21.3 26.7	x	x	7.6 ± 0.66	x		22	28	2.69 ± 0.169	0.77
		Unweighted	$\bar{x}$	24.6			8.4			23.0		[2]2.58	0.785
		1974[1]	48	17.9 22.0 29.2			7.8 ± 0.67			23	30	2.83 ± 0.179	0.79

[1]Including counts of *Cymatogaster gracilis*
[2]Difference between unweighted means of mainland and island values significant at P = 0.05

TABLE 4.—Analysis of variance of kelp-bed fish counts ($\log_{10}$ transformed) and species counts from cinetransects composing yearly samples filmed during 1971-74 in canopy and bottom habitats. For the two-way ANOVA's, samples were classified by sites (Santa Barbara mainland and Santa Cruz Island, southern California) and years (four sequential Septembers). For the one-way ANOVA's, samples were classified by years for each site separately (Mainland and Island subheads).

Source	df	Fish counts MS	Fish counts F	Species counts MS	Species counts F
Canopy:					
Sites, S	1	0.062	1	17.631	6.17**
Years, Y	3	2.802	16.78***	32.629	11.42***
SY	3	1.079	6.46***	46.414	16.24***
Error	267	0.167		2.858	
Mainland:					
Years	3	1.598	8.93***	19.744	8.37***
Error	125	0.179		2.360	
Island:					
Years	3	2.282	14.56***	59.298	17.99***
Error	142	0.157		3.296	
Bottom:					
Sites, S	1	0.001	<1	2.777	<1
Years, Y	3	1.408	19.51***	106.177	18.07***
SY	3	0.420	5.83***	19.187	3.26*
Error	345	0.072		5.877	
Mainland:					
Years	3	1.505	23.48***	88.720	15.99***
Error	164	0.064		5.547	
Island:					
Years	3	0.322	4.05**	36.639	5.93***
Error	181	0.080		6.176	

*$P \approx 0.02$; **$P \approx 0.01$; ***$P < 0.001$.

ples, on the other hand, included relatively more black perch, pile perch, and rainbow seaperch, *Hypsurus caryi*. Whereas one species—the black perch—usually dominated mainland samples, several species—the kelp bass; opaleye; blacksmith; garibaldi; and California sheephead—were often equally abundant in island samples. This more equitable spread of numbers over several common species resulted in significantly greater species diversity ($\bar{h}$) by increasing the evenness component (J) (Table 3), and is reflected in the flattened tops of dominance-diversity curves (Figure 3). Neither total species (Table 3, S) nor mean number of species per transect (Table 3, species counts) were significantly larger (Table 4) in island samples.

Mainland and island study sites differed significantly in certain characteristics of structural habitat (Table 5). Scored relief of reef bottom was significantly greater at the island site, although scored densities of giant kelp and bottom algae did not differ significantly between sites. Even though depth of reef over which bottom transects were filmed did not differ significantly between sites, it was more variable at the island site (Table 5) because the shore there sloped more steeply (Figure 4). Discounting 1973, when water at the island site was unusually turbid, underwater visibility was significantly greater by some 2.0 m at the island site (Table 6). Island water temperatures were significantly greater, though only slightly so, in all yearly sampling periods except 1973.

Yearly Differences

Species composition of bottom assemblages at mainland and island sites was more uniform (showed greater resemblance among years) than the corresponding canopy assemblages (Table 2), although significantly so only for the island site (t-tests, I between habitats, $P < 0.05$; tau, $P < 0.002$). Consequently, both measures of yearly resemblance (I, tau) of bottom-species arrays within sites were significantly greater than those between sites (Table 2). Furthermore, among-year variances of both resemblance measures for mainland- and island-bottom assemblages were less than those for both canopy assemblages, though significantly so only for island measure tau (F-test, $P \approx 0.05$). Comparing bottom assemblages only, the island assemblage was significantly more uniform (t-tests, I between sites, $P \approx 0.05$; tau, $P < 0.001$).

Fish and species counts also reflected the greater annual variability of canopy assemblages. We computed coefficients of variation (CV)—percentage ratios of standard deviation to

TABLE 5.—Means of habitat variables measured with each cinetransect for all bottom samples filmed during 1971-74 at mainland and Santa Cruz Island study sites off Santa Barbara, southern California. Scored from 1 (low) to 5 (high), plant density, other algae includes all understory forms. Time of day is the 4-yr range of median times at which transects making up yearly samples were filmed. CV is coefficient of variation and CI, confidence interval. Significance levels are from Mann-Whitney U-tests of rank differences between mainland and island values.

Site	No. of observations (n)	Time of day (h)	Mean bottom type score	Mean plant density score: Giant kelp	Mean plant density score: Other algae	Bottom depth (m): $\bar{x}$ ± 95% CI	Bottom depth (m): CV	Underwater visibility (m): $\bar{x}$ ± 95% CI	Underwater visibility (m): CV
Mainland	168	1205-1403	3.89	2.43	3.16	8.62 ± 0.205	15.4%	6.11 ± 0.157	17.4%
Island	185	1210-1400	4.43**	2.29	3.29	8.28 ± 0.400	32.8%	[1]8.11 ± 0.439	[1]34.8%

**$P = 0.01$.
[1] $n = 130$, excluding unusually low values for 1973 (see Table 6).

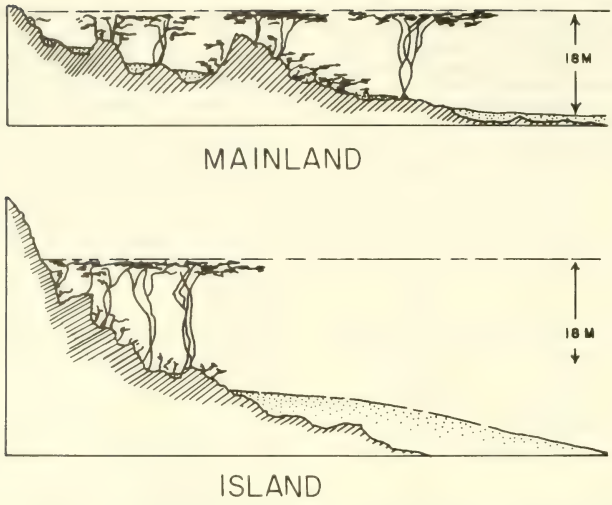


FIGURE 4.—Offshore profiles (vertically exaggerated) at mainland (Naples Reef) and Santa Cruz Island (Fry's Harbor) study sites off Santa Barbara, southern California. Off the mainland, broad sand and cobble flats (stippled) separate rocky outcrops (hatched) between the shore and Naples Reef (highest outcrop), 1.6 km offshore. Off the island, the relatively steep rocky bottom meets sand within only about 50 m of shore.

TABLE 6.—Yearly means (±95% confidence interval) of diver estimated underwater visibility and temperature measured with each cinetransect in bottom-habitat samples filmed during 1971-74 at mainland and Santa Cruz Island study sites off Santa Barbara, southern California.

Site	Year	*n*	Underwater visibility (m)	Water temperature, surface (°C)	Thermocline depth (m)
Mainland	1971	25	5.61±0.436	16.51±0.309	8.90±0.704
	1972	45	7.07±0.222	18.00±0.081	8.72±0.219
	1973	55	6.43±0.317	17.31±0.060	8.72±0.326
	1974	43	4.97±0.347	19.16±0.076	8.78±1.036
Island	1971	37	7.96±0.363	19.42±0.063	10.00±0.329
	1972	45	8.84±0.991	18.56±0.335	10.45±0.951
	1973	55	2.97±0.082	16.63±0.250	Undetected
	1974	48	7.56±1.070	19.56±0.070	·10-11

mean—to compare variability of these different measures of different magnitudes (Sokal and Rohlf 1969:62). Averaged among eight yearly samples (four mainland + four island, summarized in Table 3), CV's for counts per transect of individuals and species in canopy samples ($\bar{x}$ = 75.5% and 36.9%) were significantly greater than corresponding values (61.1%, 29.0%) for bottom samples (t-tests, $P<0.05$). Expectedly, therefore, the CV for species diversity ($\bar{h}$) of canopy samples was also significantly greater ($\bar{x}$ = 33.8% vs. 13.6%, approximate t-test, unequal variances, $P<0.05$).

Yearly differences in mean fish and species counts per transect (canopy and bottom) were highly significant (Table 4). All one-way ANOVA's revealed such differences (Table 4), and highs and lows generally coincided between mainland and island sites (Table 3). For example, counts were generally high in 1972, low in 1973, and intermediate in 1971 and 1974. Thus, most of the significant differences between means were due to a relatively abrupt decline from high counts in 1972 to low counts in 1973. The 1972 peak was most pronounced at the mainland site, when 10 of 16 species had greatest abundances, vs. 7 at the island (Table 7). Peaks of five species coincided: *Paralabrax clathratus*, *D. vacca*, *E. lateralis*, *S. atrovirens*, and *S. mystinus*. The only other coincident peak abundance was of *S. serranoides* in 1973. Despite the general correspondence between sites of overall changes in abundance and species number, however, significant year-site interactions (Table 4) indicated notable exceptions. For example, 1973 counts of individuals and species were relatively high in the mainland canopy, but low in the island canopy (Table 3).

Wolda's (1978) measures of annual variation revealed overall trends in species abundances

TABLE 7.—Annual variation of estimated density (individuals per hectare) of common kelp-bed fish species at mainland and Santa Cruz Island study sites off Santa Barbara, southern California. Variance \ n, the variance of square roots of yearly densities, measures yearly variability discounting effects of means; $\bar{R}$ at bottom of table, the mean of log R's—the average difference in $\log_{10}$ density for the species array between two successive years, measures net change in the array; AV, the variance of log R's, measures the scope of change. Between-year totals yield these statistics for an array of all 32 log R's (See text and Wolda 1978). A dash (—) indicates that the number was too small for analysis.

	Mainland					Island				
Species	1971	1972	1973	1974	Variance \ n	1971	1972	1973	1974	Variance \ n
Paralabrax clathratus	377	384	171	121	19.3	214	329	301	220	3.1
Girella nigricans	204	246	53	59	19.2	340	272	128	167	10.6
Medialuna californiensis	97	132	39	153	8.1	21	19	13	26	0.4
Brachyistius frenatus	—	—	—	—	—	2,161	1,394	299	190	247.9
Damalichthys vacca	103	109	60	62	2.1	47	70	47	39	0.8
Embiotoca jacksoni	260	512	383	339	7.3	137	117	82	101	1.3
E. lateralis	28	154	35	32	11.6	37	61	48	36	0.7
Hypsurus caryi	27	66	70	231	18.0	—	—	—	—	—
Rhacochilus toxotes	67	43	15	10	5.5	5	30	14	16	1.8
Chromis punctipinnis	864	1,207	689	657	17.4	1,872	1,420	140	976	187.5
Hypsypops rubicundus	—	—	—	—	—	208	273	108	167	6.6
Oxyjulis californica	161	336	280	194	6.6	71	185	143	260	10.4
Pimelometopon pulchrum	25	95	20	14	7.4	213	189	109	113	4.5
Sebastes atrovirens	11	74	15	10	6.7	154	229	124	204	3.3
S. carnatus &										
S. chrysomelas	25	17	29	31	0.4	10	23	19	12	0.6
S. mystinus	238	2,379	531	470	217.3	11	472	175	203	57.2
S. serranoides	11	26	66	29	3.9	85	102	481	145	34.3
Oxylebius pictus	27	38	29	38	0.3	—	—	—	—	—
$\bar{R}$ Between years	0.29		−0.30	0.00		0.23		−0.24	0.06	
Between-year total			0.15					0.14		
AV Between years	0.12		0.12	0.06		0.20		0.12	0.09	
Between-year total			0.11					0.15		
Mean variance, midwater planktivores					117.3					164.2
Mean variance, all others					8.3					6.0

(Table 7). In general, mean log R's (Table 7, $\bar{R}$), which measure net annual change between species arrays, differed significantly within (t-tests, $P<0.01$), but not between ($P>0.05$) sites. This further indicated that species abundances varied concordantly on both sides of the Channel. For the mainland site, $\bar{R}$ for 1971-72 was positive, indicating net increases in most species between these years (Table 7) as total fish counts increased significantly both in canopy and bottom habitats (Table 3); was negative for 1972-73 as numbers decreased in both habitats; and was zero for 1973-74 as a decrease in total canopy numbers offset an increase in bottom numbers. Net annual changes at the island site were somewhat less marked (Table 7), and numbers of fish differed significantly between 1972 and 1973 only (Table 3). In general, variances of log R's (Table 7, AV), which measure the scope of annual differences between species arrays, did not differ significantly either within or between sites (F-tests, $P>0.1$). However, the within-site differences were more marked, which is consistent with the concordance of annual trends of the mainland and island sites.

Much of the yearly variation in fish abundance was due to fluctuations in species that aggregate in the kelp canopy, especially midwater planktivores (Table 7). The average among-year variance of transformed numbers of three abundant planktivores (*B. frenatus*, *Chromis punctipinnis*, and *S. mystinus*) was relatively large (145.4, $n = 5$); that for abundant species whose vertical distributions are somewhat broader (*Paralabrax clathratus*, *G. nigricans*, *S. serranoides*, and *O. californica*) was substantially less (13.4, $n = 8$); while that for abundant demersal species (*E. jacksoni*, *Hypsypops rubicundus*, and *Pimelometopon pulchrum*) was smaller still (5.4, $n = 5$).

Yearly differences were loosely related to underwater visibility, water temperature, and, perhaps, to kelp density in the canopy. Water was relatively clear and warm during September 1972 (Table 6) when counts of individuals and of species were high. Furthermore, water was turbid and cool at the island site during 1973 when counts were low. However, at the mainland site in 1973, where no such conditions prevailed (Table 6), bottom counts were also low (Table 3). Kelp density seemed to affect canopy counts at the mainland site, where lower scores for kelp density in 1974 (Table 5) coincided with lower counts of fish in the canopy (Table 3).

In sum, variation in composition (order of relative or ranked species abundances) was less

between years than between habitats or sites, although canopy assemblages maintained less site-specific integrity than bottom assemblages. Coincident peak abundances of several species at both sites in 1972 contributed to significant yearly differences in fish counts, although significant year-site interactions revealed exceptions to the generally concordant annual trends. Fishes that aggregated in the canopy habitat, especially midwater planktivores, probably contributed most to annual variation measured by between-year log ratios of numbers per species. Yearly differences in fish abundances were loosely related to water clarity and temperature and kelp density, but correlations were not clear-cut.

DISCUSSION

Sampling

With limited time, personnel, and budget, visual transecting may be the most appropriate method for sampling fish populations in the complex reef environment, so long as it is understood that this method always underestimates densities of small, hidden, and/or cryptic species (Brock 1954; Jones and Chase 1975). Although some investigators aver that destructive methods (poisoning, dynamiting) provide broader sampling (Randall 1963; Goldman and Talbot 1976), others counter that visual methods are more representative because they record individuals of larger, stronger species that escape the slaughter (Smith and Tyler 1973). Hence, a thorough census of covert and overt species probably requires both methods (Quast 1968c).

Cinetransecting is analogous to visual transecting. Both methods may miss most covert fish (Alevizon and Brooks 1975), but record most overt individuals. For example, the rank order of species abundances from all mainland-bottom samples (Table 1) correlated significantly (tau = 0.66, $P<0.001$) with that of daytime visual transects made along a transect line about the reef crest at this site throughout the year (Ebeling and Bray 1976: table 3). Four of the five top-ranking species were the same in both studies, even though cinetransects covered a much broader area.

However, cinetransects have some advantages over visual transects. They can be made quickly, as many as 50/d in the present study. Cinetransects provide permanent records of the fish and their environment, not only for greater accuracy in identifying and counting fish, but also for reuse in related studies (see Alevizon 1975; Bray and Ebeling 1975; Love and Ebeling 1978). Diver photographers can proceed slowly and steadily, not diverting their attention from sampling to record observations or follow a transect line. They do not need extensive training in quick recognition of fish species and numbers, so can be replaced by others if required; if cinetransect samples are sorted into subsets, each filmed by one or the other of two different divers, correlations between the corresponding diver-specific species arrays are very high. For example, the four habitat-site-specific samples filmed by two divers in 1973, when sorted to eight diver-specific subsets, gave tau rank correlations ranging from 0.71 to 0.89 ($P<0.001$).

Within broad limits, furthermore, water visibility and light levels probably do not appreciably affect the volume of water sampled by cinetransects filmed along the bottom. At a given focus distance, the camera lens' depth of field is inversely related to the diameter of its aperture. In bright light, the aperature is small, creating a greater zone in which objects are in focus. In the kelp forest, however, light was generally so dim, even on clear days, that the aperture was almost always fully open. Thus, shading probably creates a fairly constant depth of field. To check this, we estimated the distance at which objects were first identifiable on film. Two divers swam along a tape measure ending in a fishlike target, one filming the target and nearby fish, the other signaling distance from target. During the first trial when underwater visibility (distance at which target was discernible) was 15.2 m, fish were identifiable on film only when photographed within about 3.5 m of the camera. During the second when visibility was only about 4.0 m, fish were still identifiable when photographed within about 3 m. Hence, the fairly constant depth of focus of the camera's lens, which was always set at 2.0 m on the distance scale, standardized the maximum distance (about 3.5 m) at which a photographed fish was identifiable.

Linear regressions of $\log_{10}$-transformed fish counts on estimated underwater visibility provide further evidence that visibility had little effect on values. Mean fish and species counts for the 1973 and 1974 island-bottom samples were similar, so the two were combined as one large sample (n = 103) for regression analysis. Although visibility varied between 2.1 and 15.2 m, the regression was nonsignificant (ANOVA F-test, P = 0.3). Even in

the canopy habitat, the effect of more variable light levels is apparently not severe. A similar regression analysis of pooled 1971-72 island-canopy samples ($n = 60$) was nonsignificant ($P = 0.9$), though visibility ranged from 4.6 to 10.7 m.

But while such inferences from camera optics and counts-visibility relations indicate that estimates of relative abundance obtained from cinetransects are comparable over a wide range of sampling conditions, we feel that the calibration of absolute densities presents difficulties. The primary problem is that, particularly in the kelp canopy, our estimates of area or volume sampled are tenuous. For this reason, we used absolute densities only for computing Wolda's (1978) measure of annual variation, which required estimated abundances per species, standardized for differences in sampling effort among years and between canopy and bottom habitats. We feel that this is proper because a systematic error in estimating will have little effect on the measure's value, which is based on yearly ratios of population sizes, not on sizes per se.

Also, combining canopy and bottom transects may miss some fish at middepth. Canopy transects covered depths between 1 and 4 m, which included the greatest concentration of fish in the upper water column. Bottom transects covered depths between the reef and about 2 m upward, which included greatest concentrations in the lower column. Nonetheless, over bottoms averaging 8.5 m deep, cinetransects generally missed the top meter as well as midwater between 4 and 6.5 m. Hence, our fish counts, even of overt midwater species, probably underestimated true abundances.

Annual Variability

Species composition (order of relative or ranked species abundances), rather than richness (number of species), contributed most to differences between mainland and island fish assemblages, which were most marked for the bottom assemblages (see also Ebeling et al. in press). Yearly mainland and island samples had the same number of species, although island species diversity was slightly greater because individuals were more evenly distributed among species. At the island site, species in a "kelp-rock" habitat group (Ebeling et al. in press)—tropically derived species such as *Pimelometopon pulchrum* and *G. nigricans*—were relatively more abundant than at Naples Reef. We had no indication that fishing intensity for such species (spear fishing, bottom angling) differed between the two sites. Nor was unnatural disturbance by kelp harvesting a factor. Furthermore, virtually unexploited kelp-rock species, such as *Hypsypops rubicundus*, were relatively more abundant at Santa Cruz Island. This indicates that much of the mainland-island difference in species composition probably reflected the observed differences in structure of natural habitat rather than differences in exploitation. Likewise, but on a broader scale, insular and continental shore-fish faunas are distinguished in the tropical western North Atlantic (Robins 1971; Gilbert 1972). Whereas turbid waters, muddy-silty bottoms, and few reefs characterize mainland habitats, clear water, coral reefs, and more stable conditions typify island habitats. Consequently, island fish assemblages contain relatively more specialized reef species, such as pomacentrids and labrids, that require the trappings and provisions of complex surfaces.

We felt that composition and abundance of the fish assemblages remained fairly constant among years, considering that they inhabit a presumed zone of faunal transition (Hubbs 1974; Horn and Allen 1978). Species composition varied more between sites and habitats than among years. This indicates that a particular assemblage persists, despite significant yearly variation in its fish and species counts. Yet we had few standards for comparison. Sale (1978:85) knew of no evidence that demonstrated "long-term local stability in reef fish communities," presumably because long-term monitoring studies were wanting. With a 7-yr study of fishes inhabiting a rocky tidal pool in the northern Gulf of California, however, Thomson and Lehner (1976) showed that fish abundance, diversity, and species order were seasonally predictable and varied little from year to year. In fact, the fish assemblage was remarkably resilient, recovering quickly from unpredictable and devastating disturbances, such as severe storms, winter kills, and rotenone poisoning. More generally, Wolda (1978) emphasized the need for actual measures of annual variability in tropical and other animal assemblages to test a plethora of theoretical speculation.

Our values of Wolda's (1978) measure of annual variation (AV) in arrays of species were in fact relatively low. AV's for fish assemblages at mainland and island sites (0.11, 0.15) did not differ significantly (F-tests of variance ratios) from most of those (0.06-0.33, averaging 0.15) for arthropods

living in humid, climatically stable and more predictable areas, but were significantly less than most values (0.12-0.64, averaging 0.34) for arthropods living in dry, climatically unstable environments (Wolda 1978: table 2). Values of AV (0.17, 0.20) that we calculated from annual sight transects of reef fishes taken off central California by Miller and Geibel (1973) and Burge and Schultz (see footnote 6) exceeded our values, but not significantly so. But our AV's were significantly less than the value (0.55) that we calculated from Livingston's (1976) trawl samples of fish from a Florida estuary during two successive winters (F-tests of variance ratios, $P<0.01$). Thus, annual variation in species abundances of our fish assemblages may be more typical of communities in relatively stable environments than of those from highly variable environments.

Climatic and other environmental anomalies may contribute to annual variation. Peak fish abundance in 1972 occurred in relatively clear and warm water, which may stimulate fish to be more active (Quast 1968a, b, c; Larson 1977), and perhaps more easily photographed. The summer and fall of 1972 followed a relatively calm winter of light rainfall (Harger 1979: append. B), and was a favorable period for growth of small benthic algae and associated animals, which are important forage for surfperches and other microcarnivores. On the other hand, poor visibility may have caused abrupt decreases in counts of *Chromis punctipinnis* at the island site in 1973. An obligatory daytime planktivore (Bray 1978), this species may seek bottom shelter when water is turbid. Generally, midwater planktivores were more variable in numbers than other species. Decreased kelp cover at the mainland site in 1974 probably drove some fish bottomward, but not necessarily out of view; an aggregate decrease of eight individuals per canopy transect of *C. punctipinnis, Paralabrax clathratus,* and *O. californica* accompanied a corresponding increase of five per bottom transect.

However, less obvious factors may be more important, because other periods of clear and warm water produced no such peak abundances. Time lags in responses of fish populations to environmental change preclude simple explanations of annual variation. Lags between bumper births and subsequent adult recruitment may cause populations to overshoot their environmental carrying capacities (Hutchinson 1978). Alternatively, fixed spawning seasons coupled with an unpredictable cycle in food production may limit recruits independently of the carrying capacity of the environment for adults (Cushing 1969). From bottom-trawl catches, Mearns[12] concluded that recruitment of juvenile nearshore fishes occurs over relatively short periods off southern California and may vary markedly in success among species from one year to the next. Larson (1977) found that counts of *S. carnatus* and *S. chrysomelas* decreased significantly at several depths in an area near the island site during 1973-76. This decrease may have been the result of sparse juvenile settlement observed in 1974-75.

Migration and predation may play a role, especially at the mainland site, a semi-isolated offshore reef; e.g., kelp perch, which are canopy specialists, occurred sporadically and sparsely there. Kelp cover has varied considerably over the years. But even though cover may vary at other places as well, the distance of this reef from extensive kelp beds inshore may have inhibited kelp-perch recolonization after periods of canopy loss. Several natural predators eat reef fishes, but we do not know if the rate varies from year to year. During the day, harbor seals and sea lions forage at both sites. Predatory fish such as kelp bass may eat relatively more young of species such as surfperches that do not hide in the reef itself, during periods when plant cover is sparse. At night, larger individuals of such prey fish may be particularly vulnerable to large Pacific electric ray, *Torpedo californica*, which invade the reef then (Bray and Hixon 1978). Love (1978) concluded that olive rockfish, which grow slowly and seldom move between reefs, are decimated chronically by overfishing. Although kelp bass are equally exploited, adult replacements apparently move in to restore a portion of a contiguous population (Quast 1968d).

It is noteworthy that the constancy or "stability" in species composition of our fish assemblages was roughly correlated with species diversity. Canopy assemblages were relatively simple, with many individuals distributed unevenly among a few species. They were less constant in composition than the bottom assemblages, which were characterized by more species and more even distribution of individuals among species. Also, the island bottom assemblage, which was the more diverse

[12]Mearns, A. J. 1977. Abundance of bottom fish off Orange County. *In* Coastal water research project, annual report 1977, p. 133-142. Southern California Coastal Water Research Project, 646 W. Pacific Coast Highway, Long Beach, CA 90806.

because of greater evenness, maintained a more constant species composition than the mainland-bottom assemblage. But there is no good basis, either theoretical (May 1973) or empirical, for assuming that this relation is a causal one. Some diverse communities of coral-reef fishes are reportedly not stable at all; in fact, fluctuations in their species composition may actually increase their diversity (Sale 1977, 1978; Talbot et al. 1978).

Rather, both constancy and diversity of the assemblages are probably determined by the type of habitat in which they live. Thus, the relatively low diversity and high temporal instability of the canopy assemblages probably reflect the simplicity and instability of the canopy habitat. Most fish meet in the canopy to eat plankton or planktivorous fishes. In this way, the canopy habitat is a concourse, where animals meet for one purpose (Elton 1927; Whittaker 1965). Here there are relatively few opportunities for diversifying form and function, and hence fewer species. Relatively few environmental factors strongly influence species distributions, as May (1975) suggested in general for simply structured communities. Ephemeral currents, turbidity, temperature, and kelp growth may influence the distribution of canopy dwellers. Bray (1978) has shown that the distribution of adult blacksmith is strongly affected by food-bearing currents. Adults have largely independent sources of food and shelter: the reef provides shelter but water currents carry in their planktonic food. Blacksmith feed in dense aggregations, and since local oceanographic conditions fluctuate rapidly (Quast 1968a) and plankton occurs in patches (Wiebe 1970), the location of their optimal area of foraging frequently shifts.

In contrast, our bottom assemblages depend on more stable commodities like rocks and infaunal prey, which are not so immediately affected by factors, like currents, that change rapidly. Many bottom species are solitary, parochial, or even territorial (Clarke 1970; DeMartini 1976; Larson 1977; Hixon 1979). Thus, their local density is not so likely to change from day to day.

The greater variability of the mainland-bottom assemblage than that of the island is curious. Perhaps the relative isolation of the mainland site may contribute to vagarious settlement of fish larvae and other recruitment (Larson 1977). Also, the mainland site has relatively large areas of reef flat and a surrounding plain of sand and cobble, creating more of a "transitional" type of habitat. Periodic occurrences of such species as the black croaker, *Cheilotrema saturnum*, and rainbow surfperch, which are atypical of continuous high-relief rocky habitats, lend discontinuity to the Naples fish assemblage.

ACKNOWLEDGMENTS

We thank Milton Love for help in taking and viewing cinetransects. Norm Lammer provided much technical assistance with equipment and boating operations. We appreciate use of the UCSB Channel Island Field Station, through the kindness of Carey Stanton who provided access, and of the U.S. Navy, Port Hueneme who provided transport. This work was sponsored by NOAA, Office of Sea Grant, Department of Commerce, under grant no. 2-35208-6 and 04-3-158-22 (Project R-FA-14); by NSF Sea Grants GH 43 and GH 95; and by NSF grants GA 38588 and OCE76-23301. Supplementary funding was provided by a UCSB Faculty Research Grant (No. 369) for computer time and by the Marine Science Institute through the courtesy of Henry Offen.

LITERATURE CITED

ALEVIZON, W. S.
1975. Spatial overlap and competition in congeneric surfperches (Embiotocidae) off Santa Barbara, California. Copeia 1975:352-356.
1976. Fishes of the Santa Cruz Island kelp forests. Oceans Mag. 9:44-49.

ALEVIZON, W. S., AND M. G. BROOKS.
1975. The comparative structure of two western Atlantic reef-fish assemblages. Bull. Mar. Sci. 25:482-490.

BRAY, R. N.
1978. Foraging migrations of the blacksmith, *Chromis punctipinnis*, a planktivorous kelp-bed fish. Ph.D. Thesis, Univ. California, Santa Barbara, 110 p.

BRAY, R. N., AND A. W. EBELING.
1975. Food, activity, and habitat of three "picker-type" microcarnivorous fishes in the kelp forests off Santa Barbara, California. Fish. Bull., U.S. 73:815-829.

BRAY, R. N., AND M. A. HIXON.
1978. Night-shocker: predatory behavior of the Pacific electric ray (*Torpedo californica*). Science (Wash., D.C.) 200:333-334.

BROCK, V. E.
1954. A preliminary report on a method of estimating reef fish populations. J. Wildl. Manage. 18:297-308.

BROWN, D. W.
1974. Hydrography and midwater fishes of three contiguous oceanic areas off Santa Barbara, California. Los Ang. Cty. Mus. Contrib. Sci. 261, 30 p.

CLARKE, T. A.
1970. Territorial behavior and population dynamics of a pomacentrid fish, the garibaldi, *Hypsypops rubicunda*. Ecol. Monogr. 40:189-212.

CLARKE, W. D., AND M. NEUSHUL.
1967. Subtidal ecology of the southern California coast. *In* T. A. Olsen and F. J. Burgess (editors), Pollution and marine ecology, p. 29-42. Wiley, N.Y.

CUSHING, D. H.
1969. The regularity of the spawning season of some fishes. J. Cons. 33:81-92.

DEMARTINI, E. E.
1976. The adaptive significance of territoriality and egg cannibalism in the painted greenling, *Oxylebius pictus* Gill, a northeastern Pacific marine fish. Ph.D. Thesis, Univ. Washington, Seattle, 272 p.

DUNNETT, C. W.
1970. Multiple comparison tests. Biometrics 26:139-141.

EBELING, A. W., AND R. N. BRAY.
1976. Day versus night activity of reef fishes in a kelp forest off Santa Barbara, California. Fish. Bull., U.S. 74:703-717.

EBELING, A. W., R. J. LARSON, AND W. S. ALEVIZON.
In press. Habitat groups and island-mainland distribution of kelp-bed fishes off Santa Barbara, California. *In* D. M. Power (editor), Multidisciplinary symposium on the California Islands. Santa Barbara Mus. Nat. Hist.

ELTON, C.
1927. Animal ecology. Sidgwick and Jackson, Lond., 209 p.

FEDER, H. M., C. H. TURNER, AND C. LIMBAUGH.
1974. Observations on fishes associated with kelp beds in Southern California. Calif. Dep. Fish Game, Fish Bull. 160, 144 p.

GILBERT, C. R.
1972. Characteristics of the western Atlantic reef-fish fauna. Q. J. Fla. Acad. Sci. 35:130-144.

GOLDMAN, B., AND F. H. TALBOT.
1976. Aspects of the ecology of coral reef fishes. *In* O. A. Jones and B. Endean (editors), Biology and geology of coral reefs 3 (Biol. 2), p. 125-154. Acad. Press, N.Y.

HARGER, B. W. W.
1979. Coastal oceanography and hard substrate ecology in a California kelp forest. Ph.D. Thesis, Univ. California, Santa Barbara, 422 p.

HEWATT, W. G.
1946. Marine ecological studies on Santa Cruz Island, California. Ecol. Monogr. 16:185-210.

HIXON, M. A.
1979. Competitive interactions and spatiotemporal patterns among California reef fishes of the genus *Embiotoca*. Ph.D. Thesis, Univ. California, Santa Barbara, 213 p.

HOBSON, E. S., AND J. R. CHESS.
1976. Trophic interactions among fishes and zooplankters near shore at Santa Catalina Island, California. Fish. Bull., U.S. 74:567-598.

HORN, M. H., AND L. G. ALLEN.
1978. A distributional analysis of California coastal marine fishes. J. Biogeogr. 5:23-42.

HUBBS, C. L.
1960. The marine vertebrates of the outer coast. Syst. Zool. 9:134-147.
1974. Review of "Marine Zoogeography" by John C. Briggs. Copeia 1974:1002-1005.

HUTCHINSON, G. E.
1978. An introduction to population ecology. Yale Univ. Press, New Haven, 260 p.

JOHNSON, R. K., AND T. S. Y. KOO.
1975. Production and distribution of striped bass (*Morone saxatilis*) eggs in the Chesapeake and Delaware Canal. Chesapeake Sci. 16:39-55.

JONES, R. S., AND J. A. CHASE.
1975. Community structure and distribution of fishes in an enclosed high island lagoon in Guam. Micronesica 11:127-148.

LARKIN, P. A.
1978. Fisheries management—an essay for ecologists. Annu. Rev. Ecol. Syst. 9:57-73.

LARSON, R. J.
1977. Habitat selection and territorial competition as the causes of bathymetric segregation of sibling rockfishes (*Sebastes*). Ph.D Thesis, Univ. California, Santa Barbara, 170 p.

LIVINGSTON, R. J.
1976. Diurnal and seasonal fluctuations of organisms in a North Florida estuary. Estuarine Coastal Mar. Sci. 4:373-400.

LOVE, M. S.
1978. Aspects of the life history of the olive rockfish, *Sebastes serranoides*. Ph.D. Thesis, Univ. California, Santa Barbara, 183 p.

LOVE, M. S., AND A. W. EBELING.
1978. Food and habitat of three switch-feeding fishes in the kelp forests off Santa Barbara, California. Fish. Bull., U.S. 76:257-271.

MAY, R. M.
1973. Stability and complexity in model ecosystems. Princeton Univ. Press, Princeton, N.Y., 235 p.
1975. Patterns of species abundance and diversity. *In* M. L. Cody and J. M. Diamond (editors), Ecology and evolution of communities, p. 81-120. Harv. Univ. Press, Camb., Mass.

MEETER, D. A., AND R. J. LIVINGSTON.
1978. Statistical methods applied to a four-year multivariate study of a Florida estuarine system. *In* K. L. Dickson, J. Cairns Jr., and R. L. Livingston (editors), Biological data in water pollution assessment: quantitative and statistical analyses, p. 53-67. ASTM (Am. Soc. Test. Mater.) Spec. Tech. Publ. 652.

MILLER, D. J., AND J. J. GEIBEL.
1973. Summary of blue rockfish and lingcod life histories; a reef ecology study; and giant kelp, *Macrocystis pyrifera*, experiments in Monterey Bay, California. Calif. Dep. Fish Game, Fish Bull. 158, 137 p.

NEUSHUL, M., W. D. CLARKE, AND D. W. BROWN.
1967. Subtidal plant and animal communities of the Southern California Islands. *In* R. N. Philbrick (editor), Proceedings of the symposium on the biology of the California Islands, p. 37-55. Santa Barbara Botanic Garden, Santa Barbara, Calif.

NIE, N. H., C. H. HULL, J. G. JENKINS, K. STEINBRENNER, AND D. H. BENT.
1975. Statistical package for the social sciences. McGraw-Hill, N.Y., 675 p.

PIELOU, E. C.
1966. The measurement of diversity in different types of biological collections. J. Theo. Biol. 13:131-144.

QUAST, J. C.
1968a. Some physical aspects of the inshore environment, particularly as it affects kelp-bed fishes. *In* W. J. North

and C. L. Hubbs (editors), Utilization of kelp-bed resources in Southern California, p. 25-34. Calif. Dep. Fish Game, Fish Bull. 139.

1968b. Fish fauna of the rock inshore zone. *In* W. J. North and C. L. Hubbs (editors), Utilization of kelp-bed resources in Southern California, p. 35-55. Calif. Dep. Fish Game, Fish Bull. 139.

1968c. Estimates of the populations and the standing crop of fishes. *In* W. J. North and C. L. Hubbs (editors), Utilization of kelp-bed resources in Southern California, p. 57-79. Calif. Dep. Fish Game, Fish Bull. 139.

1968d. Observations on the food and biology of kelp bass, *Paralabrax clathratus* with notes on its sportfishery at San Diego, California. *In* W. J. North and C. L. Hubbs (editors), Utilization of kelp-bed resources in Southern California, p. 81-108. Calif. Dep. Fish Game, Fish Bull. 139.

RANDALL, J. E.

1963. An analysis of the fish populations of artificial and natural reefs in the Virgin Islands. Caribb. J. Sci. 3:31-47.

ROBINS, C. R.

1971. Distributional patterns of fishes from coastal and shelf waters of the tropical western Atlantic. *In* Symposium on investigations and resources of the Caribbean Sea and adjacent regions. Pap. Fish. Res., p. 249-255. FAO, Rome.

SALE, P. F.

1977. Maintenance of high diversity in coral reef fish communities. Am. Nat. 111:337-359.

1978. Coexistence of coral reef fishes—a lottery for living space. Environ. Biol. Fishes 3:85-102.

SMITH, C. L., AND J. C. TYLER.

1973. Direct observation of resource sharing in coral reef fish. Helgol. wiss. Meeresunters. 24:264-275.

SNEATH, P. H. A., AND R. R. SOKAL.

1973. Numerical taxonomy: the principles and practice of numerical classification. W. H. Freeman, San Franc., 573 p.

SOKAL, R. R., AND F. J. ROHLF.

1969. Biometry. The principles and practice of statistics in biological research. W. H. Freeman, San Franc., 776 p.

TALBOT, F. H., B. C. RUSSELL, AND G. R. V. ANDERSON.

1978. Coral reef fish communities: unstable, high-diversity systems? Ecol. Monogr. 48:425-440.

THOMSON, D. A., AND C. E. LEHNER.

1976. Resilience of a rocky intertidal fish community in a physically unstable environment. J. Exp. Mar. Biol. Ecol. 22:1-29.

WHITTAKER, R. H.

1965. Dominance and diversity in land plant communities. Numerical relations of species express the importance of competition in community function and evolution. Science (Wash., D.C.) 147:250-260.

WIEBE, P. H.

1970. Small-scale spatial distribution in oceanic zooplankton. Limnol. Oceanogr. 15:205-217.

WOLDA, H.

1978. Fluctuations in abundance of tropical insects. Am. Nat. 112:1017-1045.

CERATIOID ANGLERFISHES OF THE PHILIPPINE ARCHIPELAGO, WITH DESCRIPTIONS OF FIVE NEW SPECIES[1]

THEODORE W. PIETSCH[2] AND JEFFREY A. SEIGEL[3]

ABSTRACT

Ceratioid anglerfishes of the Philippine Archipelago, an area bounded by the islands of the Philippines to the north, Malaysia and Sumatra to the west, and New Guinea to the east, represent 10 of the 11 ceratioid families, 22 genera and 42 species, 5 species of which are newly described forms of the genus *Oneirodes* (Oneirodidae). The vast bulk of this material has recently been provided by midwater collections made by the *Alpha Helix* during the 1975 Southeast Asian Bioluminescence Expedition. All known records of ceratioids are listed with keys to families, genera, and species represented in the area. Revised and supplemental diagnostic and descriptive data as well as notes on geographic distribution are also provided.

Our knowledge of the ceratioid anglerfish fauna of the Philippine Archipelago, an area bounded by the islands of the Philippines to the north, Malaysia and Sumatra to the west, and New Guinea to the east, has recently been broadly expanded by midwater collections made by the RV *Alpha Helix* during the 1975 Southeast Asian Bioluminescence Expedition. This collecting effort was the first major ichthyological survey of this part of the world since the historic cruises of the United States Fisheries steamer *Albatross* in 1907-09, and the Danish RV *Dana* in 1929. The Ceratioidei are now represented by 10 of the 11 families, 22 genera, and 42 species, 5 species of which are newly described forms of the genus *Oneirodes* (Oneirodidae). All known records of ceratioids from this area are listed below with keys to families, genera, and species. Revised and supplemental diagnostic and descriptive data as well as notes on geographic distribution are also provided.

METHODS AND MATERIALS

Standard lengths (SL) are used throughout. Methods for taking counts and measurements, and terminology used in describing escal morphology follow Pietsch (1974a, fig. 60). Terminology used in describing the various parts of the angling apparatus follows Bradbury (1967). Definitions of terms used for the different stages of development follow Bertelsen (1951). Locality data for *Alpha Helix* stations that yielded ceratioid material are listed in Appendix 1. *Alpha Helix* collections were made with a rectangular midwater trawl of 8 m^2 mouth area (RMT-8) that was equipped with an opening and closing device. This gear is more fully described elsewhere (Clarke 1969; Baker et al. 1973; Hopkins et al. 1973). All *Alpha Helix* material was deposited in the Natural History Museum of Los Angeles County (LACM). Material from other sources is catalogued in the following institutions: Australian Museum, Sydney (AMS), Scripps Institution of Oceanography, La Jolla (SIO), National Museum of Natural History, Washington, D.C. (USNM), and the Zoological Museum, University of Copenhagen (ZMUC). Specimens are females unless otherwise stated.

KEY TO FEMALES OF THE FAMILIES OF SOUTHEAST ASIAN CERATIOIDEI

1A. No distal bulb, illicium tipped with filaments; longest rays of dorsal and anal fin >60% of SL ..... Caulophrynidae

1B. A bulbose light organ on tip of illicum; longest rays of dorsal and anal fin much <60% SL 2

2A. More than 11 dorsal fin rays ..... Melanocetidae

2B. Less than 11 dorsal fin rays 3

3A. Two or three caruncles on back; cleft of mouth vertical to very oblique . Ceratiidae

[1]Contribution No. 540 from the College of Fisheries, University of Washington, Seattle, WA 98195.

[2]College of Fisheries, University of Washington, Seattle, WA 98195.

[3]Section of Ichthyology, Natural History Museum of Los Angeles County, Los Angeles, CA 90007.

Manuscript approved October 1979.
FISHERY BULLETIN: VOL. 78, NO. 2, 1980.

3B. No caruncles on back; cleft of mouth nearly horizontal 4
4A. A second cephalic ray present immediately posterior to base of illicium, bearing a distal luminous gland (withdrawn beneath skin in larger specimens, its presence indicated by a small pore) ..... Diceratiidae
4B. No second cephalic ray 5
5A. Upper jaw extending anteriorly far beyond lower jaw; esca with 1-3 denticles ..... Thaumatichthyidae
5B. Jaws equal anteriorly; esca without denticles 6
6A. Illicium emerging on tip of snout; length of head <35% SL; length of caudal peduncle >20% SL; 5 pectoral radials ..... Gigantactinidae
6B. Illicium emerging behind tip of snout; length of head >35% SL; length of caudal peduncle <20% SL; 3 or 4 pectoral radials 7
7A. Dermal spines or plates present 8
7B. Skin naked 10
8A. Skin with some large, bony plates, each bearing a median spine ..... Himantolophidae
8B. Skin with numerous, close set spines .. 9
9A. Teeth present on ceratobranchials 1-4; 4 pectoral radials (but fusing to 3 in specimens greater than about 150 mm SL); larvae and adolescents up to about 50 mm SL with a short, digitiform, hyoid barbel ..... Centrophrynidae
9B. Ceratobranchial teeth absent; 3 pectoral radials; no hyoid barbel ..... Oneirodidae (*Spiniphryne*)
10A. Six branchiostegal rays; more than 4 dorsal fin rays; anal fin rays 4-7 ..... Oneirodidae
10B. Four to five branchiostegal rays; 3 dorsal fin rays, rarely 2 or 4; anal fin rays 2-4 ..... Linophrynidae

CAULOPHRYNIDAE

Key to Females of Genera and Species of Southeast Asian Caulophrynidae

1A. Illicium short, less than SL; dorsal fin rays 14-22; anal fin rays 12-19 ..... *Caulophryne pelagica* (Brauer)
1B. Illicium long, 268% of SL in a 41 mm SL specimen; dorsal fin rays 6, anal fin rays 5 ..... *Robia legula* Pietsch (known from only the holotype, 41 mm SL)

Caulophryne Goode and Bean 1896

Caulophryne pelagica (Brauer 1902)

Material.—LACM 36023-1, 13 mm SL, stn 143.

A single individual, representing the sixth known specimen of *C. pelagica*, and the first record of this species from southeast Asian waters, was collected by the *Alpha Helix* in 1975. It was included in a recent revision of the family (Pietsch 1979).

Caulophryne sp. A

Material.—LACM 36025-1, female 98 mm SL with parasitic male 12 mm SL, stn 37.

This female and parasitically attached male, collected from the Banda Sea, cannot be placed within the material of any of the three recognized species of *Caulophryne* (Pietsch 1979). The attached male represents the second example of sexual parasitism in the family Caulophrynidae.

Caulophryne sp. B, Figure 1

Material.—LACM 36112-1, 10 mm SL, stn 183; LACM 36111-1, 10.5 mm SL, stn 184; LACM 36109-2, 11.5 mm SL, stn 193.

These three small females were sorted out of the *Alpha Helix* collections after a recent revision of the family went to press (Pietsch 1979). They differ significantly from the material of the three recognized species of *Caulophryne* in having an elongate, distally branched, lateral appendage on each side of the escal bulb; distal escal filaments, present in all the described species of the genus, are absent. Although these most likely represent a new form, the small size of the specimens and their poor condition do not warrant description at this time.

Robia Pietsch 1979

Robia legula Pietsch 1979

Material.—LACM 36024-1, 41 mm, stn 81 (holotype).

This species is known from a single specimen collected in the Banda Sea (Pietsch 1979).

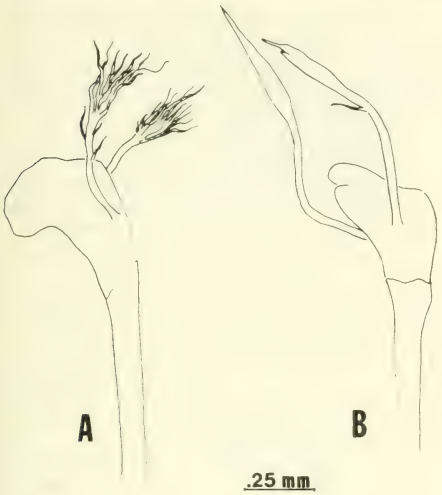


FIGURE 1.—Escae of *Caulophryne* sp. B, left lateral views: A. LACM 36112-1, 10 mm SL; B. LACM 36111-1, 10.5 mm SL.

MELANOCETIDAE

Melanocetus Günther 1864

Key to Females of Species of Southeast Asian *Melanocetus*

1A. Anterior margin of vomer nearly straight; width of pectoral fin lobe 10.7-17.8% SL; number of lower jaw teeth 32-78 .... *M. johnsoni* Günther

1B. Anterior margin of vomer deeply concave; width of pectoral fin lobe 6.1-8.9% SL; number of lower jaw teeth 46-142 .... *M. murrayi* Günther

Melanocetus johnsoni Günther 1864

Material.—LACM 36076-3, 14 mm SL, stn 26; LACM 36059-3, 15 mm SL, stn 103; LACM 36032-3, 15 mm SL, stn 110; LACM 36076-5, 17 mm SL, stn 26; LACM 36074-2, 18 mm SL, stn 120; LACM 36033-2, 36 mm SL, stn 88.

Six specimens of *M. johnsoni* were collected by the *Alpha Helix* in 1975, all of which were included in a recent revision of the Melanocetidae (Pietsch and Van Duzer 1980). This species has a wide geographic distribution in tropical and subtropical waters of all three major oceans of the world.

Melanocetus murrayi Günther 1887

Material.—LACM 36114-1, 68 mm SL, stn 66; LACM 36113-1, 82 mm SL, stn 71; LACM 36115-1, 84 mm SL, stn 102.

Melanocetus murrayi is represented by three females in the *Alpha Helix* collections (Pietsch and Van Duzer 1980). This species has a wide horizontal distribution in the Atlantic and Pacific Oceans, but is apparently absent from the Indian Ocean.

Melanocetus sp.

Material.—Males: LACM 36067-2, 13.5 mm SL, stn 23; LACM 36116-1, 21.5 mm SL, stn 84; LACM 36032-4, 22.5 mm SL, stn 110.

These male specimens could not be satisfactorily identified to species (Pietsch and Van Duzer 1980).

HIMANTOLOPHIDAE

Himantolophus Reinhardt 1837

Himantolophus sp.

Material.—Female: LACM 36038-3, 2(12.5-14 mm SL), stn 87. Males: LACM 36091-4, 16 mm SL, stn 142; LACM 36057-4, 19 mm SL, stn 93; LACM 36075-4, 4(19.5-21 mm SL), stn 121; LACM 36074-3, 21 mm SL, stn 120; LACM 36040-3, 27.5 mm SL, stn 27; LACM 36046-8, 2(29.5-33 mm SL), stn 97; LACM 36124-1, 31 mm SL, stn 112.

Thirteen specimens of *Himantolophus* were collected by the *Alpha Helix* from the Banda, Ceram, and Halmahera Seas. The genus is cosmopolitan in all three major oceans of the world (Bertelsen 1951), yet no adult females have been collected in the immediate area. These males and larval females could not be identified specifically.

DICERATIIDAE

Key to Genera and Species of Southeast Asian Diceratiidae

1A. Illicium <50% SL; distance between insertion of illicium and symphysial car-

tilage of upper jaw <15% SL ..... *Diceratias bispinosus* (Günther)

1B. Illicium >80% SL; distance between insertion of illicium and symphysial cartilage of upper jaw >30% SL ..... *Phrynichthys thele* Uwate

Diceratias Günther 1887

Diceratias bispinosus (Günther 1887)

Material.—LACM 36075-1, 20 mm SL, stn 121.

A single specimen of *Diceratias bispinosus* was collected by the *Alpha Helix* in the Halmahera Sea. This species is known only from the Indo-West Pacific (Uwate 1979).

Phrynichthys Pietschmann 1926

Phrynichthys thele Uwate 1979

Material.—LACM 36077-1, 32 mm SL, stn 155 (holotype); LACM 36076-1, 22 mm, stn 26 (paratype).

This species is known only from two specimens collected from the Ceram and Halmahera Seas, and described in a recent revision of the Diceratiidae (Uwate 1979).

ONEIRODIDAE

Key to Females of Genera of Southeast Asian Oneirodidae

1A. Skin covered with numerous, close set spines ..... *Spiniphryne* Bertelsen

1B. Skin naked 2

2A. Sphenotic spines present; opercle deeply notched posteriorly 3

2B. Sphenotic spines absent; opercle only slightly concave posteriorly ..... *Chaenophryne* Regan

3A. Pectoral fin lobe short and broad, shorter than longest pectoral fin rays 4

3B. Pectoral fin lobe long and narrow, longer than longest pectoral fin rays ..... *Chirophryne* Regan and Trewavas

4A. Lower jaw with a symphysial spine, ventral margin of dentaries at symphysis convex; caudal fin rays not internally pigmented 5

4B. Lower jaw without symphysial spine, ventral margin of dentaries at symphysis concave; caudal fin rays internally pigmented ..... *Pentherichthys* Regan and Trewavas

5A. Illicial apparatus emerging from between frontal bones 6

5B. Illicial apparatus not emerging from between frontal bones but between sphenotic spines or further posterior ..... *Lophodolos* Lloyd

6A. Dorsal margin of frontal bones strongly curved; subopercle short and broad, lower part nearly circular 7

6B. Dorsal margin of frontal bones nearly straight; subopercle long and narrow, lower part strongly oval ..... *Dolopichthys* Garman

7A. Caudal fin rays covered with black skin for some distance beyond fin base; anal fin rays 5, rarely 4 8

7B. Caudal fin rays not coverd by black skin except at base; anal fin rays 4, rarely 5 ..... *Oneirodes* Lütken

8A. Cleft of mouth extending past eye; length of escal bulb more than half length of illicial bone; upper part of subopercle broad and rounded ..... *Microlophichthys* Regan and Trewavas

8B. Cleft of mouth not extending past eye; escal bulb considerably shorter than half length of illicial bone; upper part of subopercle slender and tapering to a point ..... *Danaphyrne* Bertelsen

Spiniphryne Bertelsen 1951

Spiniphryne gladisfenae (Beebe 1932)

Material.—LACM 36073-2, 18 mm SL, stn 94.

Spiniphryne gladisfenae was previously known only from the Atlantic Ocean (Bertelsen and Pietsch 1975): three specimens collected from the eastern tropical Atlantic, and the holotype from off Bermuda. A fifth specimen, collected in the Banda Sea by the *Alpha Helix*, is the first record from the Pacific.

Oneirodes Lütken 1871

Key to Females of Species of Southeast Asian *Oneirodes*

Oneirodes melanocauda, known only from five larval specimens is omitted from the following key.

1A. Epibranchial of first arch toothed ..... *O. carlsbergi* (Regan and Trewavas)
1B. Epibranchial teeth absent 2
2A. Anterior escal appendage without internal pigment; usually two pairs of filamentous anterolateral escal appendages ..... (*O. schmidti* group) .. 3
2B. Anterior escal appendage internally pigmented; anterolateral escal appendages, if present, one or four filamentous pairs 5
3A. Length of all escal appendages less than length of escal bulb ..... *O. micronema* Grobecker
3B. Length of some escal appendages much greater than length of escal bulb 4
4A. Anterior escal appendage unbranched, anterolateral escal appendages absent .. .. *O. alius* Seigel and Pietsch
4B. Anterior escal appendage highly branched, anterolateral escal appendages present .. *O. schmidti* (Regan and Trewavas)
5A. Medial escal appendages present 6
5B. Medial escal appendages absent 10
6A. Posterior escal appendage cylindrical in cross section 7
6B. Posterior escal appendage compressed .. 8
7A. Anterior escal appendage cylindrical in cross section; posterior escal appendage as long as or longer than length of escal bulb ..... *O. eschrichtii* Lütken
7B. Anterior escal appendage laterally compressed; posterior escal appendage less than half length of escal bulb ..... *O. sabex* n.sp.
8A. Medial escal appendages short and closely set in a tight cluster 9
8B. Medial escal appendages elongate and widely placed ..... *O. thysanema* n.sp
9A. Anterior escal appendage elongate and cylindrical in cross section, with a few short, distal branches; pectoral fin rays 17 ..... *O. pterurus* n.sp.
9B. Anterior escal appendage short and laterally compressed, with a membranous scalloped distal margin; pectoral fin rays 13 or 14 ..... *O. cristatus* (Regan and Trewavas)
10A. Anterior escal appendage directed dorsally; posterior escal appendage as long as or longer than length of escal bulb ...11
10B. Anterior escal appendage directed anteroventrally; posterior escal appendage much shorter than length of escal bulb ..... *O. plagionema* n.sp.
11A. Posterior escal appendage unbranched, length two to four times length of escal bulb .. *O. flagellifer* (Regan and Trewavas)
11B. Posterior escal appendage branched, approximately as long as length of escal bulb ..... *O. schistonema* n.sp.

Oneirodes carlsbergi (Regan and Trewavas 1932)

Material.—LACM 36068-2, 19 mm, stn 25.

Oneirodes carlsbergi is known from the western tropical Atlantic and Pacific Oceans, and from a single record in the Indo-West Pacific region at about lat. 17° N, long. 120° E (Pietsch 1974a, fig. 107). An additional specimen, collected by the *Alpha Helix* from the Banda Sea, is the second known record from this part of the world.

Oneirodes cristatus (Regan and Trewavas 1932), Figure 2

Oneirodes cristatus is known only from the type material (3 females, 20-165 mm SL) collected by the *Dana* in the Banda and Celebes Seas (Pietsch 1974a).

Oneirodes eschrichtii Lütken 1871, Figure 3

Material.—LACM 36049-1, 10.5 mm SL, stn 194; LACM 36122-2, 12 mm SL, stn 179; LACM 36121-2, 21 mm SL, stn 178.

Oneirodes eschrichtii has a nearly cosmopolitan

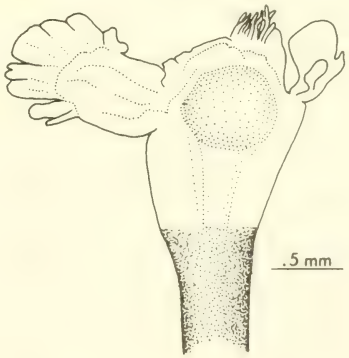


FIGURE 2.—Esca of *Oneirodes cristatus*, lectotype, ZMUC P9286, 165 mm SL, left lateral view.

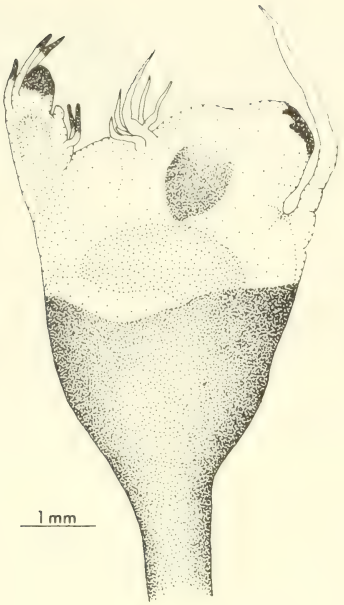


FIGURE 3.—Esca of *Oneirodes eschrichtii*, holotype, ZMUC P64, 153 mm SL, left lateral view.

distribution (Pietsch 1974a, fig. 109). Three specimens of this species were collected by the *Alpha Helix* in southeast Asian waters.

Oneirodes flagellifer (Regan and Trewavas 1932), Figure 4, Table 1

Material.—LACM 36118-1, 2(10.5-13.5 mm SL), stn 180; LACM 36117-1, 11.5 mm SL, stn 173;

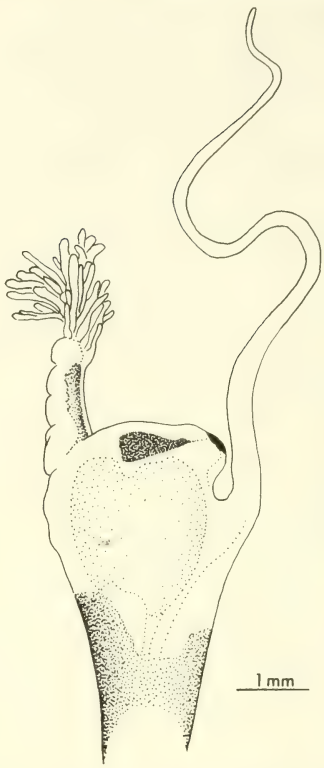


FIGURE 4.—Esca of *Oneirodes flagellifer*, holotype, ZMUC P9280, 22 mm SL, left lateral view.

LACM 36100-2, 12 mm SL, stn 166; LACM 36112-2, 14 mm SL, stn 183; LACM 36109-3, 15.5 mm SL, stn 193.

TABLE 1.—Measurements and counts of specimens of *Oneirodes flagellifer*. Measurements expressed as percentage of standard length.

Item	LACM 36118-1	LACM 36117-1	LACM 36100-2	LACM 36118-1	LACM 36112-2	LACM 36109-3
Standard length (mm)	10.5	11.5	12	13.5	14	15.5
Length:						
Head	—	43.5	41.7	46.1	46.4	45.2
Lower jaw	—	47.8	45.8	46.1	50.0	48.4
Premaxilla	—	34.8	33.3	37.0	35.7	32.3
Illicium	23.8	21.7	—	22.2	25.0	19.3
Head depth	—	43.5	41.7	37.0	46.4	45.2
Teeth:						
Vomer	4	6	6	6	6	7
Upper jaw	16	19	17	28	42	42
Lower jaw	22	30	28	36	45	48
Dorsal fin rays	—	6	5	5	5	5
Anal fin rays	4	4	4	—	4	4
Pectoral fin rays	—	—	15	15	15	14

Oneirodes flagellifer was previously known from only three specimens, all collected from the Indo-West Pacific region: the holotypes of *O. flagellifer* and *O. thysanophorus* (= *O. flagellifer*) collected by the *Dana* in 1929, and an additional specimen collected by the *Galathea* in 1951 (Pietsch 1974a, fig. 110). The *Alpha Helix* has added six additional females from the Sulu Sea that compare very well with the previously recorded material (Table 1).

Oneirodes melanocauda Bertelsen 1951

Oneirodes melanocauda is known from five larval specimens (easily separated from other *Oneirodes* larvae by the presence of pigment on the tips of the caudal fin rays, Pietsch 1974a) three of which were collected by the *Dana* in southeast Asian waters. No additional material was provided by the Southeast Asian Bioluminescence Expedition.

Oneirodes plagionema n.sp., Figures 5, 6; Table 2

Material.—A single female, the holotype, LACM 36114-2, 25 mm SL, stn 66.

Diagnosis.—A species of *Oneirodes* differing from all previously described species in escal morphology: anterior appendage narrow, elongate, and directed anteroventrally; medial appendages absent; posterior appendage minute; a pair of filamentous, branched, anterolateral appendages.

Description.—Escal appendage pattern B (Pietsch 1974a, fig. 60B); esca with anterior appendage narrow and elongate, with a single, short, distal filament, directed anteroventrally; medial appendages absent; terminal papilla unusually large, rounded, with a distal pigment spot; posterior appendage minute; a filamentous, branched, anterolateral appendage on each side (Figure 5).

Suboperculum short, upper end rounded without indentation on posterior margin (Figure 6); length of lower fork of operculum 24.0% of SL; ratio of lengths of upper and lower forks of operculum 0.53.

Epibranchial teeth absent; teeth present on pharyngobranchial II.

Counts and measurements in Table 2.

Etymology.—The name *plagionema* is derived from the Greek *plagios*, meaning oblique, and *nema*, thread, alluding to the oblique, anteroventrally directed anterior escal appendage.

FIGURE 5.—Esca of *Oneirodes plagionema* n.sp., holotype, LACM 36114-2, 25 mm SL, left lateral view.

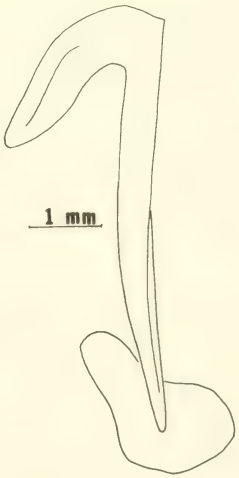


FIGURE 6.—Opercular bones of *Oneirodes plagionema* n.sp., holotype, LACM 36114-2, 25 mm SL, right lateral view.

TABLE 2.—Measurements and counts of four new species of *Oneirodes*. Measurements expressed as percentage of standard length.

Item	*O. plagionema* Holotype LACM 36114-2	*O. pterurus* Holotype LACM 36075-3	*O. schistonema* Holotype LACM 36036-3	*O. thysanema* Paratype LACM 36073-4	*O. thysanema* Holotype USNM 207931
Standard length (mm)	24	30	74	13	26.5
Length:					
Head	45.8	46.7	37.2	38.5	45.3
Lower jaw	45.8	50.0	41.2	42.3	47.2
Premaxilla	31.2	35.0	26.3	26.9	30.2
Illicium	25.0	26.7	28.4	15.4	26.4
Head depth	37.5	46.7	28.4	34.6	43.4
Teeth:					
Vomer	5	6	6	4	6
Upper jaw	24	30	42	8	32
Lower jaw	35	39	40	10	30
Dorsal fin rays	5	6	6	5	6
Anal fin rays	4	4	4	4	4
Pectoral fin rays	15	17	14	17	17

Oneirodes pterurus n.sp., Figures 7, 8; Table 2

Material.—A single female, the holotype, LACM 36075-3, 30 mm SL, stn 121.

Diagnosis.—A species of *Oneirodes* differing from all previously described species in escal morphology: anterior appendage with a few distal branches; medial appendage represented by a tuft

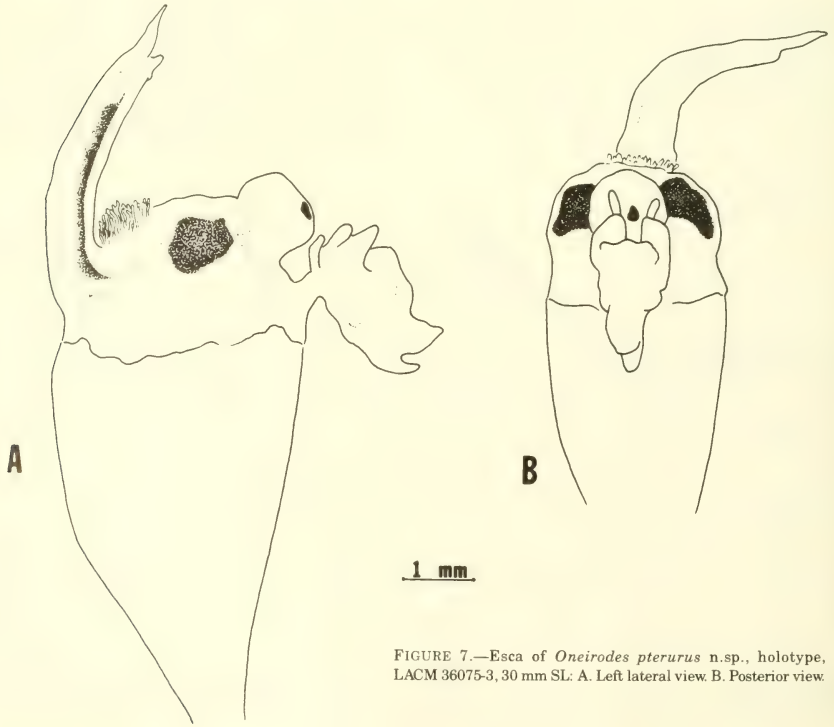


FIGURE 7.—Esca of *Oneirodes pterurus* n.sp., holotype, LACM 36075-3, 30 mm SL: A. Left lateral view. B. Posterior view.

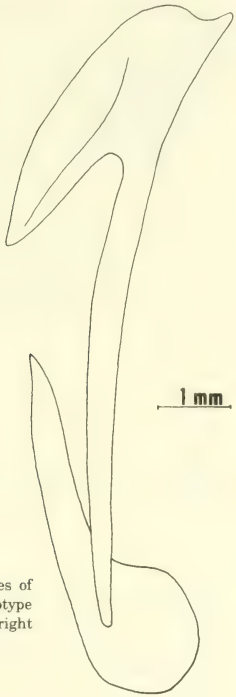


FIGURE 8.—Opercular bones of *Oneirodes pterurus* n.sp., holotype LACM 36075-3, 30 mm SL, right lateral view.

of short filaments; posterior appendage nonfilamentous.

Description.—Escal appendage pattern B (Pietsch 1974a, fig. 60B); esca with anterior appendage approximately as long as escal bulb, bearing three, short branches at distal tip; distal end of internal, pigmented tube of anterior appendage with a circular, translucent "eye-spot"; medial appendage represented by a tuft of extremely short filaments; terminal papilla bulbous, with a distal pigment spot; posterior appendage nonfilamentous, consisting of a large, compressed wedge of tissue on a short, narrow base, bearing two or three, short filaments on each side of anterior surface, and two winglike projections, one above the other, on posterior margin; anterolateral appendages absent (Figure 7).

Suboperculum unusually long and narrow, upper end tapering to a point without indentation on posterior margin (Figure 8); length of lower fork of operculum 27.3% of SL; ratio of lengths of upper and lower forks of operculum 0.56.

Epibranchial teeth absent; teeth present on pharyngobranchial II.

Counts and measurements in Table 2.

Etymology.—The name *pterurus* is derived from the Greek *pteron*, meaning wing, and *ura*, tail, alluding to the winglike posterior escal appendage of this species.

Oneirodes sabex n.sp., Figures 9, 10; Table 3

Oneirodes eschrichtii Pietsch 1974a:100, 103, fig. 116B (misidentification).

Material.—Fourteen metamorphosed females, 12-121 mm. Holotype: LACM 36116-3, 46 mm SL, stn 84. Paratypes: LACM 36087-4, 3(12-26.5 mm SL), stn 135; LACM 36068-3, 12 mm SL, stn 25; LACM 36028-5, 13 mm SL, stn 141; LACM 36023-3, 13 mm SL, stn 143; LACM 36089-4, 2(15-17 mm SL), stn 137; LACM 36051-3, 15 mm SL, stn 38; LACM 36088-4, 15.5 mm SL, stn 136; AMS I.20315-010, 32.5 mm SL, *Kapala*, lat. 33°53′ S, long. 152°02′ E, Engel Midwater Trawl, 0-900 m, bottom depth 1,800 m, 1330-1990 h, 14 December 1977; AMS I.20314-016, 39 mm SL, *Kapala*, lat. 33°28′ S, long. 152°33′ E, Engel Midwater Trawl, 0-900 m, bottom depth 4,200 m, 0530-1045 h, 14 December 1977; SIO 70-339, 121 mm SL, lat. 19°35′ N, long. 122°57′ E, 3 m IKMT (Isaacs-Kidd Midwater Trawl), 0-1,450 m, 1845-0225 h, 15-16 September 1970.

Diagnosis.—A species of *Oneirodes* differing from all previously described species in escal morphology: anterior appendage noncylindrical, compressed, without pigmented, internal tube; medial appendage present; posterior appendage cylindrical, unbranched.

Description.—Escal appendage pattern B (Pietsch 1974a, fig. 60B); esca with anterior appendage noncylindrical, strongly compressed and rounded, darkly pigmented along distal margin in some specimens; a pair of filamentous medial appendages; terminal papilla usually with two distal pigment spots situated on midline, one just behind the other; posterior appendage short, stout, and cylindrical; anterolateral appendages absent (Figure 9; Pietsch 1974a, fig. 116B).

Suboperculum short, upper end tapering to a

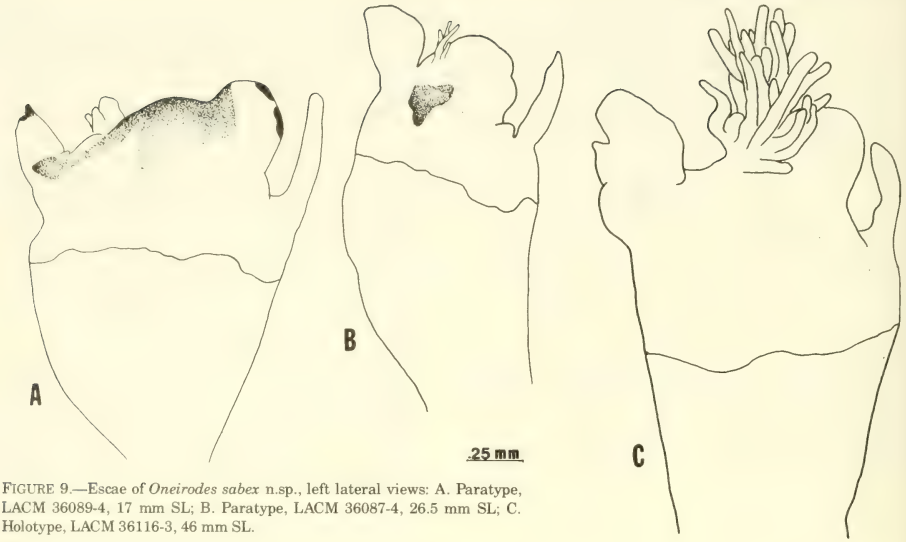
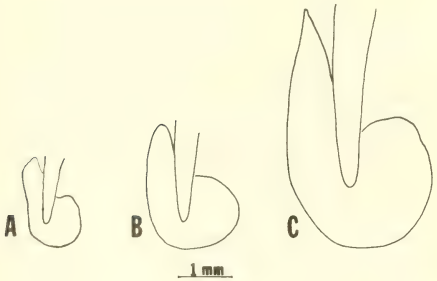


FIGURE 9.—Escae of *Oneirodes sabex* n.sp., left lateral views: A. Paratype, LACM 36089-4, 17 mm SL; B. Paratype, LACM 36087-4, 26.5 mm SL; C. Holotype, LACM 36116-3, 46 mm SL.



point without indentation on posterior margin (Figure 10); length of lower fork of operculum 27.1% of SL; ratio of lengths of upper and lower forks of operculum 0.48.

Epibranchial teeth absent; teeth present on pharyngobranchial II.

Counts and measurements in Table 3.

FIGURE 10.—Subopercula of *Oneirodes sabex* n.sp., right lateral views: A. Paratype, LACM 36089-4, 17 mm SL; B. Paratype, AMS I.20315-010, 32 mm SL; C. Holotype, LACM 36116-3, 46 mm SL.

TABLE 3.—Measurements and counts of specimens of *Oneirodes sabex* n.sp. Measurements expressed as percentage of standard length.

Item	LACM 36068-3	LACM 36028-5	LACM 36087-4	LACM 36089-4	LACM 36051-3	LACM 36088-4	LACM 36089-4	Paratype LACM 36087-4	Holotype LACM 36116-3	Paratype SIO 70-339
Standard length (mm)	12	13	13	15	15	15.5	17	26.5	45.5	121
Length:										
Head	41.7	46.1	38.5	43.3	40.0	41.9	35.3	39.5	37.4	35.1
Lower jaw	45.8	42.3	42.3	46.7	43.3	48.4	35.3	45.3	41.8	36.7
Premaxilla	29.2	30.8	30.8	33.3	30.0	32.3	23.5	32.1	27.5	26.0
Illicium	20.8	19.2	19.2	26.7	23.3	29.0	17.6	26.5	18.7	14.4
Head Depth	41.7	38.5	38.5	43.3	40.0	45.2	35.3	41.5	38.5	34.2
Teeth:										
Vomer	4	4	4	8	4	6	4	6	6	6
Upper jaw	5	15	—	22	23	34	25	30	26	42
Lower jaw	5	26	21	30	30	34	25	37	41	50
Dorsal fin rays	6	5	6	6	6	6	6	5	6	6
Anal fin rays	4	4	4	4	4	4	4	4	4	4
Pectoral fin rays	—	16	16	15	15	16	17	15	14	16

Distribution.—*Oneirodes sabex* is known only from southeast Asian and eastern Australian waters: the *Alpha Helix* material, including the holotype and 10 paratypes, was collected in the Banda Sea; the 121 mm SL paratype (SIO 70-339) is from off Luzon, Philippines; the 32.5 and 39 mm SL paratypes (AMS I. 20315-010, AMS I.20314-016) were collected off Sydney, Australia.

Etymology.—The name *sabex* is an acronym formed from the initial letters of the name "Southeast Asian Bioluminescence Expedition" in recognition of the important ichthyological contribution made by those involved.

Oneirodes schistonema n.sp., Figures 11, 12; Table 2

Material.—A single female, the holotype, LACM 36036-3, 74 mm, stn 24.

Diagnosis.—A species of *Oneirodes* differing from all previously described species in escal morphology: anterior appendage branched, unpigmented internally; medial and anterolateral appendages absent; posterior appendage branched.

Description.—Escal appendage pattern B (Pietsch 1974a, fig. 60B); esca with a stout, unpigmented, anterior appendage, less than length of escal bulb, bearing four, short, distal branches; pigmented internal tube of anterior appendage absent; medial and anterolateral appendages absent; terminal papilla without distal pigment spot; posterior appendage as large as anterior appendage, bearing four short branches near distal end (Figure 11).

Upper end of suboperculum long, narrow, and tapering, left suboperculum deeply indented (Figure 12); length of lower fork of operculum 25.3% of SL; ratio of lengths of upper and lower forks of operculum 0.48.

Epibranchial teeth absent; teeth present on pharyngobranchial II.

Counts and measurements in Table 2.

Etymology.—The name *schistonema* is derived from the Greek *schistos*, meaning divided, and *nema*, thread, alluding to the divided anterior and posterior escal appendages of this species.

Oneirodes thysanema n.sp., Figures 13, 14; Table 2

Material.—Two females, 13 and 26.5 mm SL. Holotype: USNM 207931, 26.5 mm SL; Ocean Acre cruise 7, stn 13N, Bermuda, lat. 32°18′ N, long. 63°30′ W, 3 m IKMT, 0-1,500 m, 1430-1730 h, 8

FIGURE 11.—Esca of *Oneirodes schistonema* n.sp., holotype, LACM 36036-3, 74 mm SL, left lateral view.

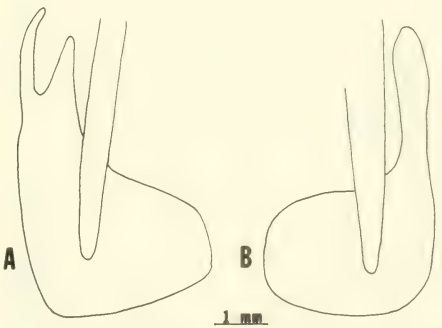


FIGURE 12.—Subopercle of *Oneirodes schistonema* n.sp., holotype, LACM 36036-3, 74 mm SL: A. Right lateral view; B. Left lateral view.

FIGURE 13.—Esca of *Oneirodes thysanema* n.sp., USNM 207931, holotype, 26.5 mm SL, left lateral view.

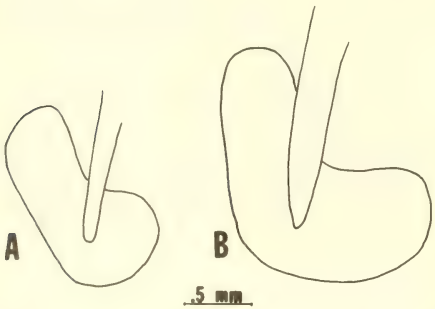


FIGURE 14.—Subopercula of *Oneirodes thysanema* n.sp., right lateral views: A. Paratype, LACM 36093-4, 13 mm SL; B. Holotype, USNM 207931, 26.5 mm SL.

September 1969. Paratype: LACM 36073-4, 13 mm SL, stn 94.

Diagnosis.—A species of *Oneirodes* differing from all previously described species in escal morphology: anterior appendage with a series of filaments along posterior margin; medial appendages in three groups; terminal papilla elongate; posterior appendage compressed and branched.

Description.—Escal appendage pattern B (Pietsch 1974a, fig. 60B); esca with a stout, internally pigmented, anterior appendage, greater than length of escal bulb, bearing along posterior margin a single branched filament proximally, and a series of unbranched filaments distally; medial appendages in three groups, a highly filamentous pair lying between a similar, but unpaired appendage, and a series of three, stout papillae situated at the base of the terminal papilla; terminal papilla unusually long, directed posterodorsally; posterior appendage as long as anterior appendage, highly compressed, bearing one or two, short, lateral filaments, and a considerably longer, branched, filamentous, anterolateral appendage on each side; distal tip of internal tube of anterior appendage, and dorsal pigment patch of escal bulb with a paired circular, translucent "eye spot" (Figure 13).

Suboperculum short and broad, upper end rounded without indentation on posterior margin (Figure 14); length of lower fork of operculum 27.7-30.2% of SL; ratio of lengths of upper and lower forks of operculum 0.48-0.50.

Epibranchial teeth absent; teeth present on pharyngobranchial II.

Counts and measurements in Table 2.

Etymology.—The name *thysanema* is derived from the Greek *thysanos*, meaning a fringe, and *nema*, thread, alluding to the numerous filaments fringing the anterior escal appendage of this species.

Oneirodes alius Seigel and Pietsch 1978,
Figure 15, Table 4

Material.—LACM 36026-1, 38 mm SL, stn 122 (holotype); LACM 36027-1, 18 mm SL, stn 147 (paratype); LACM 36028-1, 21 mm SL, stn 141

TABLE 4.—Measurements and counts of specimens of *Oneirodes alius*. Measurements expressed as percentage of standard length.

Item	LACM 36089-2	LACM 36091-2	LACM 36091-2	LACM 36096-2
Standard length (mm)	10	11.5	11.5	12
Length:				
Head	45.0	39.1	39.1	37.5
Lower jaw	40.0	43.5	43.5	45.8
Premaxilla	20.0	21.7	26.1	25.0
Illicium	20.0	17.4	17.4	16.7
Head depth	40.0	34.8	34.8	33.3
Teeth:				
Vomer	4	4	4	4
Upper jaw	—	—	—	14
Lower jaw	—	—	18	16
Dorsal fin rays	5	5	7	6
Anal fin rays	4	4	4	4
Pectoral fin rays	15	—	15	16

FIGURE 15.—Esca of *Oneirodes alius*, holotype, LACM 36026-1, 38 mm SL, left lateral view.

(paratype); LACM 36089-2, 10 mm SL, stn 137; LACM 36091-2, 2(11.5 mm SL), stn 142; LACM 36096-2, 12 mm SL, stn 150.

Oneirodes alius, a member of the *O. schmidti* group (Pietsch 1974a), was originally described from three specimens collected by the *Alpha Helix* in the Halmahera Sea (Seigel and Pietsch 1978). After the description went to press, four additional specimens were sorted out from *Alpha Helix* stations made in approximately the same localities as the type-material. In all respects, these specimens compare well with the original description.

Oneirodes schmidti (Regan and Trewavas 1932), Figures 16, 17; Table 5

Material.—LACM 36031-3, 15.5 mm SL, stn 58; LACM 36057-3 2(65-92 mm SL), stn 93; LACM 36067-3, 78 mm SL, stn 23.

The 1975 Southeast Asian Bioluminescence Expedition of the *Alpha Helix* provided the first representatives of *O. schmidti* since the capture of the holotype by the *Dana* in 1929. The new material compares well with the type-specimen in all characters, except for some minor differences in escal morphology. The species is redescribed below based on the new *Alpha Helix* material.

Description.—Escal appendage pattern C (Pietsch 1974a, fig. 60C); esca with a large, complex anterior appendage consisting of a wide, compressed base bearing a relatively short, unpaired and branched filament on posterior margin, two extremely long, distal filaments (about 16.3 to 17.3% of SL) that bifurcate as many as five times, and a stout, bifurcated, medial filament each branch of which becomes highly branched distally; a pair of filamentous, highly branched, medial appendages less than length of escal bulb; terminal papilla

TABLE 5.—Measurements and counts of *Oneirodes schmidti*. Measurements expressed as percentage of standard length.

Item	LACM 36031-3	LACM 36067-3	LACM 36057-3	LACM 36057-3
Standard length (mm)	15.5	78	92	65
Length:				
Head	45.2	44.9	46.2	47.7
Lower jaw	51.7	51.3	52.7	52.3
Premaxilla	38.7	35.9	36.4	40.0
Illicium	35.5	107.7	91.3	87.7
Head depth	38.7	46.1	42.4	46.1
Teeth:				
Vomer	4	6	5	5
Upper jaw	29	66	67	62
Lower jaw	36	57	56	65
Dorsal fin rays	6	6	5	6
Anal fin rays	4	4	4	4
Pectoral fin rays	16	16	17	16

FIGURE 16.—Esca of *Oneirodes schmidti*, LACM 36057-3, 65 mm SL, left lateral view.

FIGURE 17.—Subopercula of *Oneirodes schmidti*, right lateral views: A. LACM 36057-3, 65 mm SL; B. LACM 36067-3, 78 mm SL; C. LACM 36057-3, 92 mm SL.

with a single, distal streak of pigment; a slender, unbranched posterior appendage less than length of escal bulb; a relatively short, filamentous, branched, anterolateral appendage on each side (the inner pair of stout, anterolateral appendages described for the holotype of *O. schmidti* by Pietsch 1974a: 78, fig. 99, correspond to the elongate, bifurcated filaments that are associated with the anterior appendage of the new material; Figure 16).

Suboperculum long and narrow, upper part tapering without indentation on posterior margin (Figure 17; Pietsch 1974a:78, fig. 98); length of lower fork of operculum 26.6-27.7% of SL; ratio of lengths of upper and lower forks of operculum 0.47-0.51.

Epibranchial teeth absent; teeth present on pharyngobranchial II.

Counts and measurements in Table 5.

Distribution.—All five known specimens of *O. schmidti*, including the holotype, were collected in the Banda Sea.

Oneirodes micronema Grobecker 1978, Figure 18.

Material.—LACM 36039-3, 89 mm SL, stn 113 (holotype); LACM 36043-3, 17 mm SL, stn 157 (paratype).

This species, a member of the *O. schmidti* group (Pietsch 1974a), was recently described by Grobecker (1978) based on two females collected in the Banda Sea.

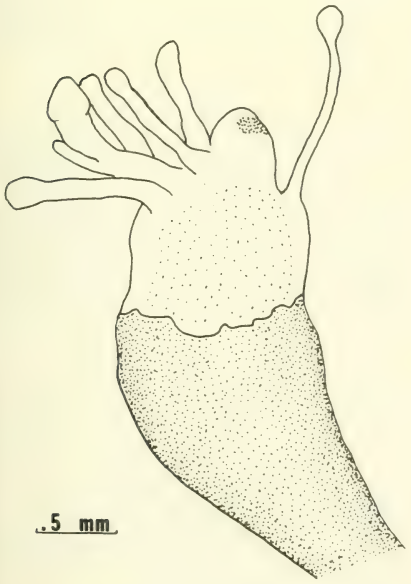


FIGURE 18.—Esca of *Oneirodes micronema*, holotype, LACM 36039-3, 89 mm SL, left lateral view.

Oneirodes sp. of *Oneirodes schmidti* Group, Bertelsen 1951

Material.—LACM 36046-6, metamorphosed female, 13 mm SK, stn 97 (illicium length 36.9% of SL).

Oneirodes sp.

Material.—Adolescent and adult males and females, and metamorphosing stages not identifiable to species or species group. Metamorphosed females representing possible new species: LACM 36087-5, 13 mm SL, stn 135 (illicium 15.4% of SL, upper jaw teeth 14, lower jaw teeth 21, pectoral fin rays 15); LACM 36089-5, 14 mm SL, stn 137 (illicium 14.3% of SL, upper jaw teeth 15, lower jaw teeth 20, pectoral fin rays 15; esca like that of LACM 36087-5); LACM 36115-2, 21 mm SL, stn 102 (illicium 23.8% of SL, upper jaw teeth 27, lower jaw teeth 38, pectoral fin rays 16). Metamorphosing females: LACM 36121-1, 2(7.5-9 mm SL), stn 178; LACM 36106-2, 8.5 mm SL, stn 187; LACM 36088-3, 9.5 mm SL, stn 136; LACM 36049-3, 9.5 mm SL, stn 194; LACM 36073-3, 10 mm SL, stn 94; LACM 36087-3, 10 mm SL, stn 135; LACM 36028-4, 10 mm SL, stn 141; LACM

36046-5, 11 mm SL, stn 97; LACM 36027-3, 11 mm SL, stn 147; LACM 36076-4, 11.5 mm SL, stn 26. Metamorphosed males: LACM 36108-2, 8.5 mm SL, stn 192; LACM 36087-2, 4(9-10 mm SL), stn 135; LACM 36081-2, 3(9.5 mm SL), stn 127a; LACM 36104-2, 2(9.5-11.5 mm SL), stn 175; LACM 36039-5, 2(10-11 mm SL), stn 113; LACM 36024-4, 3(10-12 mm SL), stn 81; LACM 36057-5, 2(10-12 mm SL), stn 93; LACM 36023-4, 4(10-12 mm SL), stn 143; LACM 36028-3, 3(10-13.5 mm SL), stn 141; LACM 36048-4, 10.5 mm SL, stn 36; LACM 36073-5, 2(10-5 mm SL), stn 94; LACM 36117-2, 10.5 mm SL, stn 173; LACM 36109-4, 10.5 mm SL, stn 193; LACM 36119-1, 2(10.5-13.5 mm SL), stn 96; LACM 36026-2, 11 mm SL, stn 122; LACM 36090-2, 3(11-12 mm SL), stn 138; LACM 36027-3, 11 mm SL, stn 147; LACM 36118-2, 11 mm SL, stn 180; LACM 36076-6, 12 mm SL, stn 26; LACM 36095-2, 12 mm SL, stn 149; LACM 36077-4, 12 mm SL, stn 155; LACM 36122-1, 12 mm SL, stn 179; LACM 36084-2, 2(12-12.5 mm SL), stn 130; LACM 36091-3, 2(12-12.5 mm SL), stn 142; LACM 36089-3, 6(12-13 mm SL), stn 137; LACM 36085-2, 3(12-14 mm SL), stn 133; LACM 36120-1, 12.5 mm SL, stn 123; LACM 36041-4, 4(12.5-13 mm SL), stn 39; LACM 36088-2, 13 mm SL, stn 136; LACM 36024-3, 13 mm SL, stn 81.

Danaphryne Bertelsen 1951

Danaphryne nigrifilis (Regan and Trewavas 1932)

Danaphryne nigrifilis is known from eight specimens, one of which (the holotype, 24 mm SL, ZMUC P92102) was collected by the *Dana* in the South China Sea (Bertelsen and Pietsch 1977). No additional material was provided by the *Alpha Helix*.

Microlophichthys Regan and Trewavas 1932

Microlophichthys microlophus (Regan 1925)

Material.—LACM 36024-7, male, 17 mm SL, stn 81; LACM 36048-3, female, 22 mm SL, stn 36; LACM 36047-3, female 29 mm SL, stn 89.

Twenty-three metamorphosed females of this species (12-99 mm SL) have been previously reported from localities in the Atlantic, Indian, and Pacific Oceans (Bertelsen and Pietsch 1977). Two additional females and a male were collected by the *Alpha Helix* in the Banda and Ceram Seas. In all respects, these specimens fall within the observed variation of *M. microlophus*.

Chirophryne Regan and Trewavas

Chirophryne xenolophus Regan and Trewavas 1932

Chirophryne xenolophus is known from only two specimens, the holotype (11 mm SL, ZMUC P9296) collected by the *Dana* in the South China Sea, and a second specimen (22 mm SL, SIO 70-306) from off Japan at about lat. 32°10′ N, long. 136°05′ E (Pietsch 1978).

Dolopichthys Garman 1899

Dolopichthys pullatus Regan and Trewavas 1932

Material.—LACM 36116-2, 113 mm SL, stn 84.

Thirty-three metamorphosed females of *D. pullatus* (10-115 mm) have been previously reported from localities in the Atlantic, the Gulf of Mexico, and the eastern Pacific and Indian Oceans (Pietsch 1972). The holotype of *D. pullatus* is the only previous record from the western Pacific. One additional specimen collected by the *Alpha Helix* from the Banda Sea constitutes the second record from the Indo-West Pacific Ocean.

Dolopichthys longicornis Parr 1927

Material.—LACM 36046-3, 8.5 mm, stn 97.

Dolopichthys longicornis was previously known from 18 metamorphosed females (14-159 mm) collected from the Atlantic, Indian, and eastern Pacific Oceans (Pietsch 1972). The holotype of *D. mucronatus* (= *D. longicornis*), collected in the South China Sea, is the only previous western Pacific record. An additional specimen was collected by the *Alpha Helix* in the Banda Sea.

Dolopichthys sp.

Material.—LACM 36071-2, metamorphosed male, 12 mm, stn 59.

Chaenophryne Regan 1925

Chaenophryne longiceps Regan 1925

Material.—LACM 36039-4, metamorphosed male, 10.5 mm, stn 113.

This species has a cosmopolitan distribution in all three major oceans of the world (Pietsch 1975).

A single male taken by the *Alpha Helix* in the Banda Sea consitutes the second record for this species in southeast Asian waters.

Chaenophryne draco Beebe 1932

Material.—LACM 36073-6, 17 mm, stn 94; LACM 36123-1, 21.5 mm, stn 80.

Chaenophryne draco has a wide distribution occurring in all three major oceans of the world (Pietsch 1975). Two metamorphosed females collected by the *Alpha Helix* in the Banda Sea constitute the first records of this species in southeast Asian waters.

Chaenophryne sp. of *Chaenophryne draco* Group

Material.—LACM 36046-7, metamorphosed male, 10 mm, stn 97.

Pentherichthys Regan and Trewavas

Pentherichthys sp.

The genus *Pentherichthys* is represented in southeast Asian waters by only two larval specimens (Bertelsen 1951). No additional material was provided by the *Alpha Helix*.

Lophodolos Lloyd 1909

Lophodolos indicus Lloyd 1909

Material.—LACM 36116-4, 69 mm, stn 84.

Twenty-two female specimens of this species were previously recorded from localities in the eastern Atlantic, and the Indian and Pacific Oceans between about lat. 4° S and 30° N (Pietsch 1974b). One additional specimen was collected by the *Alpha Helix* in the Banda Sea.

Oneirodidae gen. et sp.?

Material.—Two metamorphosing males: LACM 36069-3, 11 mm, stn 28; LACM 36039-3, 11.5 mm, stn 113.

These two metamorphosing males cannot be reasonably placed within any known oneirodid genus. Both are very similar in having the following characteristics:

Description.—Nostrils opening forward; skin between anterior nostrils lightly pigmented; posterior nostril well separated from eye; operculum deeply notched posteriorly; suboperculum short and broad, upper end rounded; inner side of suboperculum darkly pigmented; subdermal pigment continuous over body to posterior margin of caudal peduncle; pectoral rays on end of a relatively short, broad lobe; dorsal fin rays 6, anal fin rays 4, pectoral fin rays 15.

Comments.—These males are similar to *Oneirodes* and *Microlophichthys* in having a short, rounded suboperculum. They differ from *Oneirodes*, however, in having the skin between the anterior nostrils lightly pigmented, the inner surface of the suboperculum darkly pigmented, and the body covered with subdermal pigment to the base of the caudal fin. On the other hand, they differ from *Microlophichthys* in the absence of a distinct, separate patch of pigment on the caudal peduncle, and in having four, instead of five anal fin rays.

THAUMATICHTHYIDAE

Thaumatichthys Smith and Radcliffe 1912

Thaumatichthys pagidostomus Smith and Radcliffe 1912

Thaumatichthys pagidostomus is known from only the holotype (60 mm SL, USNM 72952) collected by the *Albatross* off Sulawesi (Bertelsen and Struhsaker 1977).

CENTROPHRYNIDAE

Centrophryne Regan and Trewavas 1932

Centrophryne spinulosa Regan and Trewavas 1932

Centrophryne spinulosa is known from 15 metamorphosed females and 2 metamorphosing males. The lectotype (39 mm SL female, ZMUC P92122), collected by the *Dana* off the northern coast of New Guinea, is the only record from the western Pacific (Pietsch 1972).

CERATIIDAE

Key to Females of Genera and Species of Ceratiidae

1A. Illicium long, much longer than bulb

of esca; 2 caruncles on back; subopercle without spine on anterior margin .... *Ceratias* sp.

1B. Illicium short, nearly completely enveloped by bulb of esca; 3 caruncles on back; subopercle with spine on anterior margin ..... *Cryptopsaras couesi* Gill

Ceratias Kröyer 1845

Ceratias sp.

Material.—LACM 36046-9, 9 mm, stn 97; LACM 36034-3, 2(10-18 mm), stn 85; LACM 36047-4, 10.5 mm, stn 89; LACM 36073-7, 11 mm, stn 94; LACM 36125-1, 12 mm, stn 72; LACM 36032-5, 13 mm, stn 110; LACM 36074-4 13.5 mm, stn 120; LACM 36076-7, 13.5 mm, stn 26; LACM 36027-4, 15 mm, stn 147; LACM 36064-2, 16.5 mm, stn 152; LACM 36058-2, 18 mm, stn 99; LACM 36029-2, 23 mm, stn 162; LACM 36093-2, 25 mm, stn 146.

Fourteen female specimens of the genus *Ceratias* were collected by the *Alpha Helix* from the Banda, Celebes, Ceram, and Halmahera Seas. All of these are adolescent females in which the diagnostic characters of the esca have not as yet developed. Since there are two, perhaps three species of *Ceratias* (Bertelsen 1951), specific identification is impossible at this time.

Cryptopsaras Gill 1883

Cryptopsaras couesi Gill 1883

Material.—LACM 36031-4, 8 mm, stn 58; LACM 36090-3, 3(8.5-12.5 mm), stn 138; LACM 36029-3, 2(9.5-10 mm), stn 162; LACM 36042-2, 10 mm, stn 74; LACM 36074-5, 10 mm, stn 120; LACM 36034-4, 10 mm, stn 85; LACM 36100-3, 10 mm, stn 166; LACM 36109-5, 10 mm, stn 193; LACM 36087-8, 2(10-10.5 mm), stn 135; LACM 36040-4, 3(10-102 mm), stn 27; LACM 36051-4, 11 mm, stn 38; LACM 36028-6, 11 mm, stn 141; LACM 36129-1, 11 mm, stn 181; LACM 36130-1, 11 mm, stn 186; LACM 36085-4, 2(11-13 mm), stn 133; LACM 36089-6, 11.5 mm, stn 137; LACM 36063-3, 11.5 mm, stn 140; LACM 36077-5, 2(11.5-12.5 mm), stn 155; LACM 36127-1, 12 mm, stn 167; LACM 36122-3, 12 mm, stn 179; LACM 36126-1, 12.5 mm, stn 18; LACM 36037-2, 12.5 mm, stn 82; LACM 36117-3, 12.5 mm, stn 173; LACM 36084-3, 6(12.5-85 mm), stn 130; LACM 36055-2, 13 mm, stn 79; LACM 36091-5, 13 mm, stn 142; LACM 36108-3, 13 mm, stn 192; LACM 36067-4, 14 mm, stn 23; LACM 36075-5, 14 mm, stn 121; LACM 36064-3, 4(14-19.5 mm), stn 152; LACM 36080-2, 16 mm, stn 126; LACM 36128-1, 19.5 mm, stn 91; LACM 36073-8, 59 mm, stn 94; LACM 36124-2, 94 mm, stn 112.

Cryptopsaras couesi has a cosmopolitan distribution in all three major oceans of the world (Bertelsen 1951). Fifty specimens were collected by the *Alpha Helix* from the Banda, Celebes, Halmahera, Sulu, and Timor Seas.

GIGANTACTINIDAE

Gigantactis Brauer 1902

Gigantactis vanhoeffeni Brauer 1902

Material.—LACM 36031-1, 17 mm, stn 58; LACM 36039-6, 2(24-31 mm), stn 113; LACM 36032-1, 25 mm, stn 110; LACM 36046-10, 26 mm, stn 97; LACM 36131-1, 32 mm, stn 51; LACM 36034-5, 34 mm, stn 85.

The *Alpha Helix* collected seven females (six metamorphosed and one in metamorphosis) of *G. vanhoeffeni*, all from the Banda Sea. These have been incorporated in a forthcoming revision of the Gigantactindae (Bertelsen et al. in press).

Gigantactis sp. Male Group II, Bertelsen et al. in press

Material.—LACM 36034-1, 2(12-12.5 mm), stn 85; LACM 36033-1, 2(13-14 mm), stn 88; LACM 36032-1, 13.5 mm, stn 110.

Gigantactis sp. Male Group IV, Bertelsen et al. in press

Material.—LACM 36030-1, 16.5 mm, stn 109.

Gigantactinidae gen. et sp.?

Material.—LACM 36024-6, male, 11.5 mm, stn 81.

This male cannot reasonably be placed within either of the two known gigantactinid genera (Bertelsen et al. in press).

LINOPHRYNIDAE

Key to Females of Genera and Species of Southeast Asian Linophrynidae

1A. Skin transparent; hyoid barbel absent;

jaw teeth small and numerous .... *Edriolychnus schmidti* Regan

1B. Skin darkly pigmented; hyoid barbel present; teeth large and few .... *Linophryne* Collett. . 2

2A. Distal escal appendages present; barbel distally divided into about 6 branches .. .. *Linophryne corymbifera* Regan and Trewavas

2B. Distal escal appendages absent; barbel unbranched .... *Linophryne trewavasae* Bertelsen

Edriolychnus Regan 1925

Edriolychnus schmidti Regan 1925

Edriolychnus schmidti is a relatively common ceratioid occurring in all three major oceans of the world (Bertelsen 1951). No additional material, however, was provided by the *Alpha Helix* in 1975.

Linophryne Collett 1886

Linophryne corymbifera Regan and Trewavas 1932

Material.—LACM 36046-11, female, 42 mm SL with parasitic male, 9.5 mm SL, stn 97.

A single female with parasitic male, representing the first known incidence of sexual parasitism in this species, was collected by the *Alpha Helix* in the Banda Sea. The specimen was referred to as *Linophryne* sp. A by Hansen and Herring (1977), and recently described and figured by Bertelsen (1978).

Linophryne trewavasae Bertelsen 1978

Material.—LACM 36116-5, female, 73.5 mm SL with parasitic male, 10.7 mm SL, stn 84 (holotype).

Linophryne trewavasae was recently described by Bertelsen (1978) from a single female with an attached male collected by the *Alpha Helix* in the Banda Sea. The specimen was referred to as *Linophryne* sp. B by Hansen and Herring (1977).

Linophryne sp. male

Material.—LACM 36088-5, a male, 15 mm SL, stn 136.

This single male specimen could not be identified to species.

ACKNOWLEDGMENTS

We thank E. Bertelsen for critically reading the manuscript and offering valuable suggestions. The following people and institutions provided material: Bruce H. Robison, Marine Science Institute, University of California Santa Barbara; Robert J. Lavenberg and Jerry W. Neumann, LACM; John R. Paxton, AMS; Robert H. Gibbs and Susan Karnella, USNM; and Richard H. Rosenblatt and Jan Pulsifer, SIO. The work was supported by National Science Foundation Grants GB-40700, DEB 76-82279 and DEB 7826540, the National Geographic Society, and PHS Biomedical Research Support Grant No. RR-07096 administered through the Graduate School Research Fund of the University of Washington.

LITERATURE CITED

BAKER, A. DE C., M. R. CLARKE, AND M. J. HARRIS.
1973. The N.I.O. combination net (RMT 1+8) and further developments of rectangular midwater trawls. J. Mar. Biol. Assoc. U.K. 53:167-184.

BEEBE, W.
1932. Nineteen new species and four post-larval deepsea fish. Zoologica (N.Y.) 13:47-107.

BERTELSEN, E.
1951. The ceratioid fishes. Ontogeny, taxonomy, distribution and biology. Dana Rep., Carlberg Found. 39. 276 p.
1978. Notes on linophrynids IV. A new species of deep-sea anglerfish of the genus *Linophryne* and the first record of a parasitic male in *Linophryne corymbifera* (Pisces, Ceratioidei). Steenstrupia 5(3):25-32.

BERTELSEN, E., AND T. W. PIETSCH.
1975. Results of the research cruises of FRV "Walther Herwig" to South America. XXXVIII. Osteology and relationships of the ceratioid anglerfish genus *Spiniphryne* (family Oneirodidae). Arch. Fischereiwiss. 26(1):1-11.
1977. Results of the research cruises of FRV "Walther Herwig" to South America. XLVII. Ceratioid anglerfishes of the family Oneirodidae collected by the FRV "Walther Herwig". Arch. Fischereiwiss. 27(3):171-189.

BERTELSEN, E., T. W. PIETSCH, AND R. J. LAVENBERG.
In press. Morphology, systematics and distribution of ceratioid anglerfishes of the family Gigantactinidae. Nat. Hist. Mus. Los Ang. Cty. Contrib. Sci.

BERTELSEN, E., AND P. J. STRUHSAKER.
1977. The ceratioid fishes of the genus *Thaumatichthys*. Osteology, relationships, distribution and biology. Galathea Rep. 14:7-40.

BRADBURY, M. G.
1967. The genera of batfishes (family Ogcocephalidae). Copeia 1967:399-422.

BRAUER, A.
1902. Diagnosen von neuen Tiefseefischen, welche von der Valdivia-Expedition gesammelt sind. Zool. Anz. 25:277-298.

CLARKE, M. R.
1969. A new midwater trawl for sampling discrete depth horizons. J. Mar. Biol. Assoc. U.K. 49:945-960.
COLLETT, R.
1886. On a new pediculate fish from the sea off Madeira. Proc. Zool. Soc. Lond. 1886:138-143.
GARMAN, S.
1899. Reports on an exploration off the west coasts of Mexico, Central and South America, and off the Galapagos Islands, in charge of Alexander Agassiz, by the U.S. Fish Commission Steamer "Albatross" during 1891, Lieut.-Commander Z. L. Tanner, U.S.N., commanding. XXVI. The fishes. Mem. Mus. Comp. Zool. Harv. Coll. 24, 431 p.
GILL, T. N.
1883. *Cryptopsaras couesi*. Forest and Stream. Nov. 8, 1883, p. 284.
GOODE, G. B., AND T. H. BEAN.
1896. Oceanic ichthyology, a treatise on the deep-sea and pelagic fishes of the world, based chiefly upon the collections made by the steamers *Blake, Albatross,* and *Fish Hawk* in the northwestern Atlantic. U.S. Natl. Mus. Spec. Bull. 2, 553 p.
GROBECKER, D. B.
1978. A new species of anglerfish, Genus *Oneirodes* (Oneirodidae), from the Banda Sea. Copeia 1978:567-568.
GÜNTHER, A.
1864. On a new genus of pediculate fish from the sea of Madeira. Proc. Zool. Soc. Lond. 1864:301-303.
1887. Report on the deep-sea fishes collected by H.M.S. *Challenger* during the years 1873-1876. Rep. Sci. Res. Voy. H.M.S. *Challenger*, Zool. 22:1-335.
HANSEN, K., AND P. J. HERRING.
1977. Dual bioluminescent systems in the anglerfish genus *Linophryne* (Pisces: Ceratioidea). J. Zool. (Lond.) 182:103-124.
HOPKINS, T. L., R. C. BAIRD, AND D. M. MILLIKEN.
1973. A messenger-operated closing trawl. Limnol. Oceanogr. 18:488-490.
KRÖYER, H.
1845. Ichthyologiske bidrag 10. *Ceratias holboelli*. Naturhist. Tidsskr. 1(2):639-649.
LLOYD, R. E.
1909. A description of the deep-sea fish caught by the R. I. M. S. Ship "Investigator" since the year 1900, with supposed evidence of mutation in *Malthopsis*. Mem. Indian Mus. (Calcutta) 2(3):139-180.
LÜTKEN, C. F.
1871. *Oneirodes eschrichtii* Ltk. en ny grønlandsk Tudsefisk. Overs. K. Dan. Vidensk. Selsk. Forh. 1871:56-74.
PARR, A. E.
1927. Scientific results of the third Oceanographic Expedition of the "Pawnee" 1927. Bull. Bingham. Oceanogr. Collect., Yale Univ. 3(1), 34 p.
PIETSCH, T. W.
1972. A review of the monotypic deep-sea anglerfish Family Centrophrynidae: taxonomy, distribution and osteology. Copeia 1972:17-47.
1974a. Osteology and relationships of ceratioid anglerfishes of the family Oneirodidae, with a review of the genus *Oneirodes* Lütken. Nat. Hist. Mus. Los Ang. Cty., Sci. Bull. 18, 113 p.
1974b. Systematics and distribution of ceratioid anglerfishes of the genus *Lophodolos* (family Oneirodidae). Breviora 425:1-19.
1975. Systematics and distribution of ceratioid anglerfishes of the genus *Chaenophryne* (family Oneirodidae). Bull. Mus. Comp. Zool. 147:75-99.
1978. A new genus and species of ceratioid anglerfish from the North Pacific Ocean with a review of the allied genera *Ctenochirichthys, Chirophryne* and *Leptacanthichthys*. Nat. Hist. Mus. Los. Ang. Cty., Contrib. Sci. 297, 25 p.
1979. Systematics and distribution of ceratioid anglerfishes of the family Caulophrynidae with the description of a new genus and species from the Banda Sea. Nat. Hist. Mus. Los Ang. Cty., Contrib. Sci. 310:1-25.
PIETSCH, T. W., AND J. P. VAN DUZER.
1980. Systematics and distribution of ceratioid anglerfishes of the family Melanocetidae with the description of a new species from the eastern North Pacific Ocean. Fish. Bull., U.S. 78:59-87.
PIETSCHMANN, V.
1926. Ein neuer Tiefseefisch aus der Ordnung der Pediculati. Anz. Akad. Wiss. Wien 63:88-89.
REGAN, C. T.
1925. New ceratioid fishes from the N. Atlantic, the Caribbean Sea, and the gulf of Panama, collected by the "Dana." Ann. Mag. Nat. Hist., Ser. 8, 8:561-567.
REGAN, C. T., AND E. TREWAVAS.
1932. Deep-sea angler-fish (Ceratioidea). Dana Rep., Carlsberg Found. 2, 113 p.
REINHARDT, J.
1837. Ichthyologiske bidrag til den grønlandske fauna. Dan. Vidensk. Selsk. Afh. 4(7):83-196.
SEIGEL, J. A., AND T. W. PIETSCH.
1978. A new species of the ceratioid anglerfish genus *Oneirodes* (Pisces: Lophiiformes) from the Indo-West Pacific. Copeia 1978:11-13.
SMITH, H. M., AND L. RADCLIFFE.
1912. Description of a new family of pediculate fishes from Celebes. Proc. U.S. Natl. Mus. 42:579-581.
UWATE, K. R.
1979. Revision of the anglerfish Diceratiidae with descriptions of two new species. Copeia 1979:129-144.

APPENDIX TABLE 1.—*Alpha Helix* stations that yielded Ceratioidei during the Southeast Asian Bioluminescence Expedition of 1975. Coordinates are for starting position only.

Station	Sea	Latitude	Longitude	Gear depth(m)	Time (h)	Date
18	Timor	8°49.8′ S	129°43.0′ E	0-550	0900-1400	20 March
23	Banda	4°39.2′ S	129°54.1′ E	0-2,000	2225-0530	26 March
24	Banda	4°39.1′ S	129°53.7′ E	0-2,000	0115-0745	28 March
25	Banda	4°16.8′ S	129°34.4′ E	0-1,800	2010-0340	28 March
26	Ceram	2°46.0′ S	127°53.7′ E	0-1,500	0150-0800	31 March
27	Ceram	2°45.3′ S	127°55.1′ E	0-2,000	0150-0800	1 April
28	Ceram	3°14.8′ S	127°38.0′ E	0-100	2035-2205	1 April
36	Banda	4°54.0′ S	129°30.5′ E	830-1,050	1440-1620	11 April
37	Banda	4°56.3′ S	129°25.5′ E	0-2,000	1900-0155	11 April
38	Banda	4°40.4′ S	129°39.0′ E	0-780	0320-0530	12 April
39	Banda	4°45.6′ S	129°51.2′ E	0-1,000	0950-1435	13 April
51	Banda	4°56.2′ S	129°50.0′ E	550-815	1545-1655	14 April
58	Banda	4°54.5′ S	129°48.4′ E	650-810	1200-1400	16 April
59	Banda	4°57.3′ S	129°44.0′ E	1,100-1,300	1555-1755	16 April
66	Banda	4°54.0′ S	129°47.5′ E	1,500-2,000	1515-1815	17 April
71	Banda	4°55.5′ S	129°39.0′ E	1,500-2,000	1048-1523	19 April
72	Banda	4°48.5′ S	129°58.0′ E	0-600	1645-1905	19 April
74	Banda	5°04.0′ S	129°54.5′ E	720-990	0041-0241	19 April
79	Banda	4°57.5′ S	129°51.0′ E	0-710	1845-2200	27 April
80	Banda	4°48.7′ S	129°47.2′ E	0-710	2314-0220	28 April
81	Banda	4°56.5′ S	129°59.5′ E	1,000-1,500	0416-0616	28 April
82	Banda	5°02.8′ S	130°07.0′ E	0-690	0745-1050	28 April
84	Banda	5°04.5′ S	130°12.0′ E	0-1,500	1400-2100	28 April
85	Banda	4°57.5′ S	130°11.7′ E	0-750	2115-0025	28 April
87	Banda	4°52.0′ S	129°50.0′ E	0-870	0915-1215	1 May
88	Banda	4°58.0′ S	129°43.0′ E	1,000-1,500	1450-1650	1 May
89	Banda	5°03.5′ S	129°41.0′ E	0-960	1820-2112	1 May
91	Banda	4°55.0′ S	130°00.0′ E	0-600	1030-1250	5 May
93	Banda	5°02.3′ S	130°19.5′ E	0-760	1650-2013	5 May
94	Banda	5°01.5′ S	130°04.6′ E	650-1,000	2245-0045	5 May
96	Banda	5°00.0′ S	129°54.0′ E	0-300	0520-0615	6 May
97	Banda	4°54.0′ S	129°42.7′ E	0-850	0700-1025	6 May
99	Banda	5°03.0′ S	129°52.0′ E	0-460	2020-2242	6 May
102	Banda	4°45.0′ S	129°19.7′ E	0-2,000	0540-1045	7 May
103	Banda	4°49.0′ S	129°31.0′ E	550-940	1415-1630	7 May
109	Banda	4°33.0′ S	129°17.0′ E	0-1,100	0030-0445	12 May
110	Banda	4°47.4′ S	129°51.8′ E	0-1,500	0945-1235	13 May
112	Banda	4°58.0′ S	129°59.5′ E	650-850	1745-1855	13 May
113	Banda	5°07.5′ S	130°08.4′ E	650-1,000	2120-2255	13 May
120	Halmahera	0°32.0′ S	129°08.3′ E	450-1,100	1125-1325	16 May
121	Halmahera	0°41.7′ S	128°55.7′ E	1,000-1,400	1730-1930	16 May
122	Halmahera	0°36.3′ S	129°03.2′ E	575-600	2240-2340	16 May
123	Halmahera	0°29.7′ S	129°02.7′ E	1,000-1,050	0205-0410	17 May
126	Halmahera	0°22.1′ S	129°01.3′ E	450-600	1042-1142	17 May
127a	Halmahera	0°04.5′ S	128°26.5′ E	0-750	1820-2155	17 May
130	Halmahera	0°06.0′ S	128°28.7′ E	600-790	0724-0933	18 May
133	Halmahera	0°05.7′ N	128°24.8′ E	0-680	1520-1833	18 May
135	Halmahera	0°06.2′ S	128°38.3′ E	820-1,000	2306-0106	18 May
136	Halmahera	0°17.4′ S	128°47.5′ E	1,000-1,250	0446-0646	19 May
137	Halmahera	0°08.9′ S	128°40.0′ E	0-960	0955-1300	19 May
138	Halmahera	0°05.1′ N	128°29.0′ E	750-900	2150-2250	19 May
140	Halmahera	0°00.6′ S	128°46.3′ E	250-320	0202-0310	20 May
141	Halmahera	0°05.0′ S	128°52.7′ E	1,000-1,100	0625-0855	20 May
142	Halmahera	0°10.5′ S	128°33.3′ E	750-1,000	1200-1400	20 May
143	Halmahera	0°14.5′ S	128°46.7′ E	1,250-1,500	1715-1930	20 May
146	Halmahera	0°36.2′ S	129°12.0′ E	420-600	0437-0537	21 May
147	Halmahera	0°40.0′ S	128°58.5′ E	0-1,200	0635-0935	21 May
149	Halmahera	0°22.5′ S	128°57.8′ E	420-600	1640-1740	21 May
150	Halmahera	0°18.5′ S	129°00.8′ E	700-1,000	2003-2203	21 May
152	Halmahera	0°13.0′ S	129°06.5′ E	180-300	0145-0345	22 May
155	Halmahera	0°38.6′ S	129°05.6′ E	680-850	1210-1400	22 May
157	Banda	4°09.6′ S	130°50.0′ E	0-840	0215-0615	24 May
162	Celebes	2°37.6′ N	124°46.5′ E	550-800	0917-1117	1 June
166	Sulu	7°10.7′ N	121°25.6′ E	660-800	0712-0900	3 June
167	Sulu	7°19.2′ N	121°20.1′ E	950-1,100	1210-1410	3 June
173	Sulu	8°06.3′ N	121°13.2′ E	730-810	0645-0845	4 June
175	Sulu	8°28.3′ N	121°15.0′ E	920-1,100	1422-1622	4 June
178	Sulu	8°47.0′ N	121°26.0′ E	790-910	0200-0330	5 June
179	Sulu	8°58.5′ N	121°42.2′ E	1,500-2,000	0605-1005	5 June
180	Sulu	9°06.0′ N	121°51.0′ E	710-790	1340-1550	5 June
181	Sulu	9°16.8′ N	122°02.2′ E	820-950	1905-2105	5 June
183	Sulu	9°24.5′ N	122°12.3′ E	690-890	0115-0215	6 June
184	Sulu	9°18.0′ N	122°10.0′ E	480-550	0355-0455	6 June
186	Sulu	9°03.7′ N	122°03.6′ E	360-640	0936-1036	6 June
187	Sulu	8°53.0′ N	122°01.5′ E	830-900	1255-1455	6 June
192	Sulu	9°08.0′ N	122°02.5′ E	800-900	0500-0700	7 June
193	Sulu	9°21.5′ N	122°14.7′ E	800-1,100	1020-1240	7 June
194	Sulu	9°28.3′ N	122°06.8′ E	0-1,500	1350-1740	7 June

EGGS AND LARVAE OF BUTTER SOLE, *ISOPSETTA ISOLEPIS* (PLEURONECTIDAE), OFF OREGON AND WASHINGTON

SALLY L. RICHARDSON,[1] JEAN R. DUNN,[2] AND NANCY ANNE NAPLIN[3]

ABSTRACT

Development of butter sole, *Isopsetta isolepis*, is described from egg through benthic juvenile, based on reared and field-collected specimens.

Isopsetta isolepis eggs are planktonic, spherical, and transparent with a narrow perivitelline space, homogeneous yolk, and no oil globule. Diameters of 80 reared eggs averaged 0.93 mm (range 0.90-0.99 mm). Using light microscopy, early and middle stage eggs are indistinguishable from those of three other pleuronectids, English sole, *Parophrys vetulus*, sand sole, *Psettichthys melanostictus*, and starry flounder, *Platichthys stellatus*, with which they cooccur. Pigment patterns distinguish late stage *I. isolepis* eggs from those of *Psettichthys melanostictus* and *Platichthys stellatus*. Because the late stages of *I. isolepis* embryos vary widely in degree and character of pigmentation, they often cannot be reliably separated from those of *Parophrys vetulus*.

Larvae are readily distinguished by three bands of melanistic pigment on the tail region of the body combined with myomere counts (39-42). Transformation from larva to juvenile takes place at about 18-23 mm. Larvae are abundant in nearshore coastal waters off Oregon and Washington in winter and spring, where they cooccur with larvae of *P. vetulus*. Recently transformed benthic juveniles of *I. isolepis* usually are found offshore rather than in the bay and nearshore habitats occupied by young juvenile *P. vetulus*.

This paper presents the first complete description of development of the butter sole, *Isopsetta isolepis* (Lockington), from egg through benthic juvenile. Larvae of this species are common in the ichthyoplankton off Oregon and Washington where they ranked fifth in overall abundance in April and May 1967 (Waldron 1972) and third in a coastal assemblage of larval fishes off Oregon in 1971-72 (Richardson and Pearcy 1977; Richardson[4]).

Isopsetta, a monotypic genus of the family Pleuronectidae, ranges from Ventura, Calif., to the Bering Sea (Miller and Lea 1972). It is usually found in coastal waters although it has been reported from the 274-366 m depth zone in western Alaska (Demory 1971; Miller and Lea 1972; Hart 1973). Adult butter sole ranked 11th and 7th in biomass of all flatfishes taken during trawl surveys off Oregon in 1971-72 and 1973-74 (Demory et al.[5]) and 6th in biomass of all flatfishes off Washington in both 1975 and 1976 (Barss et al.[6]). Because it is a relatively small, <55 cm TL (total length), slender fish (Miller and Lea 1972; Hart 1973), it is currently of only minor commercial importance.

Levings (1968) briefly described *I. isolepis* eggs as single, nonadhesive, transparent, spherical, without an oil globule, with a mean egg diameter of 1.013 mm, although he did not illustrate them. The eggs sank at salinities ≤26.61‰ but floated at salinities ≥28.03‰. Levings concluded that the eggs were demersal within Skidegate Inlet, British Columbia, where bottom salinities were 24.96‰. *Isopsetta isolepis* larvae 4.8, 7.9, 10.0, and 15.5 mm long from Puget Sound were sketched by Blackburn (1973) but were labeled *Lyopsetta exilis*. He also provided short descriptions.

[1]School of Oceanography, Oregon State University, Corvallis, Oreg.; present address: Gulf Coast Research Laboratory, Ocean Springs, MS 39564.

[2]Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112.

[3]Northeast Fisheries Center Sandy Hook Laboratory, National Marine Fisheries Service, NOAA, Highlands, NJ 07732.

[4]Richardson, S. L. 1977. Larval fishes in ocean waters off Yaquina Bay, Oregon: abundance, distribution, and seasonality, January 1971 to August 1972. Oreg. State Univ., Sea Grant Coll. Prog., Publ. ORESU-T-77-003, 73 p.

[5]Demory, R. L., M. J. Hosie, N. TenEyck, B. O. Forsberg. 1976. Marine resource surveys on the continental shelf off Oregon, 1971-74. Oreg. Dep. Fish Wildl., Completion Rep., June 1976, 49 p.

[6]Barss, W. H., R. L. Demory, N. TenEyck. 1977. Marine resource surveys on the continental shelf and upper slope off Washington, 1975-76. Oreg. Dep. Fish Wildl., Completion Rep., September 1977, 34 p.

Manuscript accepted December 1979.
FISHERY BULLETIN: VOL. 78, NO. 2, 1980.

METHODS

Eggs from ripe fish collected in Bellingham Bay, Wash., were artificially fertilized on 12 March 1974 and were reared at the Mukilteo field station of the Northwest and Alaska Fisheries Center (NWAFC), National Marine Fisheries Service (NMFS), NOAA, Seattle, Wash. The eggs were incubated in 0.6 or 1.0 l glass beakers containing local Puget Sound seawater maintained at 9°-10° C. Subsamples of eggs were preserved in Formalin[7] in eight time periods, 4, 9, 20, 24, 48, 72, 96, and 120 h, after fertilization. Subsamples of larvae were preserved for each of 13 time periods: at hatching (144 h or 6 d after fertilization) and at 2, 3, 4, 7, 9, 11, 14, 16, 18, 21, 23, and 25 d after hatching. Although rotifers (*Brachionus plicatilus*) were added to the containers at various levels (4, 8, and 16 rotifers/ml seawater), the larvae did not feed actively and all were dead by 22 April 1974.

Approximately 300 larvae were obtained from NWAFC collections made off coastal Washington in 1972. An additional 107 larvae were obtained from Oregon State University (OSU) ichthyoplankton collections taken off the Oregon coast from 1971 to 1972 (Richardson and Pearcy 1977; Richardson see footnote 4). Benthic juveniles were collected in beam trawls off the mouth of the Columbia River in June and September 1975 (Richardson et al.[8]).

Counts of meristic structures were made on 209 larvae (3.2-23.6 mm) and 7 juveniles (44-160 mm) taken from the OSU and NWAFC collections. Larvae were stained with Alizarin Red S using Taylor's (1967) enzyme method to determine sequence of ossification. Some (45) were subsequently restained with Alcian Blue and Alizarin Red using techniques described by Dingerkus and Uhler (1977). Counts were made of dorsal fin rays, anal fin rays, caudal fin rays, left and right pectoral fin rays, branchiostegal rays, gill rakers, vertebral centra, neural spines, and haemal spines. Fin rays and vertebrae were counted even if they were tinted only slightly with alizarin stain. Uptake and retention of alizarin in ossified structures may vary depending upon the length of time the specimens have been in preservative. Differential loss of stain may account for some of the variation observed in the onset of ossification of certain structures such as teeth.

Measurements were made using an ocular micrometer in a stereomicroscope. The greatest outside diameter and greatest yolk diameter were recorded for 80 eggs from the reared series, 10 for each of the eight time periods that eggs were preserved from 4 to 120 h after fertilization. Measurements were made on 63 reared larvae, 5 specimens (when available) from each of the 13 time periods after hatching (6 d after fertilization) that larvae were preserved to 25 d after hatching. Size range of reared specimens was 2.7-5.3 mm SL (standard length). Measurements also were made on 107 larvae from plankton collections including 5 specimens (when available) for each 1.0 mm size class interval from 2 to 23 mm SL (range 2.9-23.6 mm). Body measurements were made on larvae as follows:

Standard length – snout tip to notochord tip until notochord is fully flexed and the posterior margin of the forming hypural elements is vertical, then to posterior margin of hypurals.

Head length – snout tip to cleithrum.

Body depth at pectoral fin base – vertical distance from dorsal body margin to ventral body margin, excluding finfold or fins, at the pectoral fin base.

Body depth at anus – vertical distance from dorsal body margin, excluding finfold or fin, to anus.

Body depth behind anus – vertical distance from dorsal body margin to ventral body margin, excluding finfolds or fins, at point immediately behind anus where body depth decreases greatly compared to depth at anus.

Body depth at caudal peduncle – before formation of caudal fin, vertical distance from dorsal body margin to ventral body margin, excluding finfolds or fins, at the posteriormost myomere; after caudal fin formation, least depth of caudal peduncle.

Snout length – snout tip to anterior margin of right eye.

Eye diameter – horizontal distance across right eyeball.

Snout to anus length – distance along body midline from snout tip to vertical through posterior margin of anus.

[7]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[8]Richardson, M. D., A. G. Carey, Jr., W. A. Colgate. 1977. The effects of dredged material disposal on benthic assemblages off the mouth of the Columbia River. Final Rep., Dep. Army Corps Eng. Contracts DACW 57-75-C-0137 and DACW 57-56-C-0092, Vicksburg, Miss., 411 p.

Upper jaw length – snout tip to posterior margin of maxillary.

Illustrations of eggs and larvae were made with the aid of a camera lucida. All specimens had been preserved in 5% Formalin. Illustrations of the caudal fin and skeletal structure were made from cleared and stained specimens.

VERIFICATION OF IDENTIFICATION

Reared eggs were fertilized from known parents, thus their identity was certain.

A series of larval specimens from plankton collections was linked together by pigment pattern. The left eye had begun to migrate in the largest specimens indicating that they were pleuronectids, the only right-eyed flatfishes occurring off Oregon and Washington. Positive identification was based on knowledge of early stages of all but one of the pleuronectids occurring in the area (Table 1) and on the following meristic characters for *I. isolepis* (Hart 1973; Ahlstrom[9]; this study):

Dorsal fin rays	=	78-92
Anal fin rays	=	58-69
Abdominal vertebrae	=	9-11, usually 10
Total vertebrae	=	39-42
Caudal fin rays	=	17-18, usually 18
Pectoral fin rays	=	11-13
Pelvic fin rays	=	6
Branchiostegal rays	=	7
Gill rakers	=	4-6 + 7-8

Additional confirmation was provided by larvae reared to yolk depletion, which were similar to the smallest specimens from the plankton samples.

DISTINGUISHING FEATURES

Early and middle stage eggs of *I. isolepis* are indistinguishable from those of English sole, *Parophrys vetulus*; starry flounder, *Platichthys stellatus*; and sand sole, *Psettichthys melanostictus*. Chorions of reared eggs are often noticeably striated, but this characteristic is not consistent among reared eggs and is rarely seen in eggs from the plankton. Thus, chorion sculpturing is not useful for identifying *I. isolepis* eggs.

[9]E. H. Ahlstrom, Senior Scientist, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, unpubl. data.

TABLE 1.—Pleuronectid flatfishes occurring off Oregon and Washington with references on early developmental stages.

Species	References
Atheresthes stomias	Pertseva-Ostroumova (1960, 1961)
Embassichthys bathybius	Richardson (in press)
Eopsetta jordani	Alderdice and Forrester (1971); Ahlstrom (unpubl. data); Richardson (in press)
Glyptocephalus zachirus	Ahlstrom and Moser (1975)
Hippoglossoides elassodon	Dekhnik (1959); Pertseva-Ostroumova (1961); Miller (1969); Alderdice and Forrester (1974) Forrester and Alderdice[1]
Hippoglossus stenolepis	Thompson and Van Cleve (1936); Pertseva-Ostroumova (1961)
Inopsetta ischyra	None
Isopsetta isolepis	Levings (1968); Blackburn (1973)
Lepidopsetta bilineata	Pertseva-Ostroumova (1961); Blackburn (1973); Richardson (in press)
Lyopsetta exilis	Blackburn (1973); Ahlstrom and Moser (1975)
Microstomus pacificus	Hagerman (1952); Ahlstrom and Moser (1975)
Parophrys vetulus	Budd (1940)[2]; Orsi (1968); Blackburn (1973); Ahlstrom and Moser (1975); Misitano (1976)
Platichthys stellatus	Orcutt (1950); Yusa (1957); Pertseva-Ostroumova (1961) as *Pleuronectes stellatus*
Pleuronichthys coenosus	Budd (1940) (as *P. decurrens*); Sumida et al. (1979)
Pleuronichthys decurrens	Budd (1940) (as *P. coenosus*); Sumida et al. (1979)
Psettichthys melanostictus	Hickman (1959); Sommani (1969)

[1]Forrester, C. R., and D. F. Alderdice. 1968. Preliminary observations on the embryonic development of the flathead sole (*Hippoglossoides elassodon*). Fish. Res. Board Can., Tech. Rep. 100, 20 p.
[2]The 6.3 mm larva is not *P. vetulus*.

Late stage eggs are readily distinguished from other northeast Pacific pleuronectids with similar size eggs by means of pigment. Embryos in late stage *P. melanostictus* eggs have scattered yolk-sac melanophores, and those of *Platichthys stellatus* have pigmented finfolds, while *I. isolepis* embryos lack pigment in both places. *Isopsetta isolepis* embryos are most similar to those of *Parophrys vetulus*. While *I. isolepis* embryos usually have several isolated ventral tail melanophores, their number is quite variable, ranging from none to many, whereas *P. vetulus* embryos have so many ventral tail melanophores that the pigment appears almost continuous. The head and anterior trunk pigment of *I. isolepis* is more dendritic and melanophores are less numerous than on *P. vetulus*. Despite these differences, variation in both ventral tail and trunk melanophores, especially in *I. isolepis*, is so great that late stage eggs of the two species cannot always be reliably separated.

Most sizes of *I. isolepis* larvae can be easily distinguished from other flatfish larvae off Oregon and Washington by their body form together with their striking pigment pattern, most notably the three bands of melanophores on the body posterior to the abdominal cavity. After notochord flexion the posteriormost band lines the base of the caudal fin, but the two other bands remain apparent through transformation to benthic juvenile. No

other flatfish larvae of similar form in the area have three such bands. The only other three-banded flatfish larva is deepsea sole, *Embassichthys bathybius*, but it hatches at about 9 mm, has over 60 myomeres, and a different elongate form (Richardson in press). The most similar appearing banded larval flatfish is the flathead sole, *Hippoglossoides elassodon*, which has four pigment bands.

Before the three pigment bands become obvious, i.e., in larvae <4 mm SL, larvae of *I. isolepis* are similar to those of *P. vetulus*. They usually are separable by the size and distribution of postanal ventral midline melanophores. Those of *I. isolepis* are small and appear more or less as a double row when viewed from the ventral surface; those of *P. vetulus* are enlarged and stellate and appear as a single row when viewed ventrally.

Newly transformed *I. isolepis* juveniles are also similar to *P. vetulus*. Before development of adult characters such as scales on the fins of *I. isolepis*, which will easily separate the two, *I. isolepis* can usually be distinguished by remnants of the larval pigment bands on the blind side. The number of gill rakers on the lower limb (Miller and Lea 1972) also will separate the two species (7-8 for *I. isolepis* and 10-13 for *P. vetulus*).

DEVELOPMENT OF EGGS (Figure 1)

Isopsetta isolepis eggs are spherical and transparent, with a narrow perivitelline space, a homogeneous yolk, and no oil globule. Although the eggs apparently sink at salinities ≤26.61‰ (Levings 1968), they are taken in our plankton samples, and live eggs floated in the rearing experiments (salinity ~26.9‰). Diameters of 80 reared eggs averaged 0.93 mm (0.90-0.99 mm), while yolk diameters averaged 0.76 mm (0.60-0.95 mm).

Embryonic development is typical of most teleosts with planktonic eggs. The stages of egg development we use correspond to the basic divisions of embryonic development used by Ahlstrom and Counts (1955), with detailed subdivisions of each stage (Naplin and Obenchain in press).

Pigmentation

Pigment first appears during the middle stage of embryonic development. At this time, distinct melanophores are scattered unevenly from the middle of the eyes posteriorly over the trunk. The

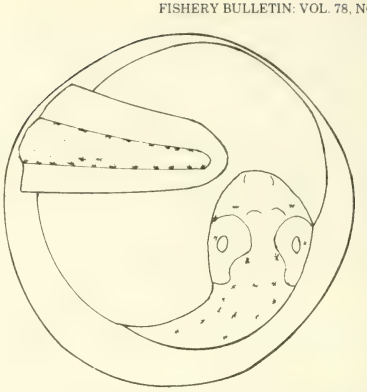


FIGURE 1.—*Isopsetta isolepis* eggs, late stage from plankton collections.

melanophores become more organized into two dorsolateral lines on the anterior somites, and diminish in size and frequency posteriorly. The dorsolateral lines are the site of melanophore formation, and pigment is present farther posteriorly as development continues.

The development of this species is unusual in that the anteriormost melanophores become increasingly dendritic and so fine that they gradually become less visible. By the time the embryos have reached the late stage (tail five-eighths of the way around the yolk), less head pigment is visible and the trunk is covered with very small but distinctly visible dendritic melanophores. Several distinct ventral melanophores lie at the juncture of the trunk and the yolk sac, and one or two isolated spots are on the yolk sac nearby. Most of the tail pigment is scattered dorsally in no obvious pattern, and several lateral melanophores are now in the ventral tail area.

When the tail is three-fourths of the way around the yolk, the head and trunk generally appear to be pigmented, although less distinctly than in the middle stage. Ventral trunk pigment is present, and some embryos may have one to three yolk-sac melanophores nearby. Scattered melanophores appear dorsally on the posterior trunk and on all surfaces of the tail. More lateral melanophores are present toward the tail tip.

From the time the tail is seven-eighths of the way around the yolk through hatching, little change in the pigment pattern occurs; however, the lateral tail melanophores have moved to become ventral. Dorsal and ventral tail pigment melanophores are

spread into thin lines between the margin of the body and finfold. The ventral melanophores are variable, ranging from no melanophores to many, and are separated at irregular intervals over the length of the tail, while the dorsal pigment can appear almost continuous. Near the tail tip the dorsal and ventral melanophores align, as in the early larvae, to form the precursor of the posteriormost band of pigment noted in the larvae.

The reared embryos appear more lightly pigmented than wild-caught embryos. In the latter, it is possible that the marked fading of the head pigment may not occur until after hatching.

Morphology

Physical development of *I. isolepis* embryos progresses as in other fishes. At the time of initial pigment formation, the blastopore has closed and the embryonic body is gradually thickening on top of the yolk sac. During this stage, the eyecups are forming, but no lens tissue is discernible. About 12 somites have formed, and Kupffer's vesicle is still visible just anterior to the tail bud.

When the tail is five-eighths of the way around the yolk, the eyecups are well-formed and lenses are present. The brain has differentiated into a forebrain and a larger midbrain. The auditory vesicles are forming but are not yet hollow. About 27 somites are present, Kupffer's vesicle is no longer visible, and the small tail has a definite finfold.

By the time the tail has reached three-fourths of the way around the yolk, the auditory vesicles are well-formed and immediately apparent. The embryo now has about 37 somites. Hatching can occur when the embryo's tail has reached seven-eighths of the way around the yolk to full circle. At this point, the embryo has the full complement of somites or myomeres (39-42) and is morphologically similar to a newly hatched larva.

DEVELOPMENT OF LARVAE (Figures 2-5)

Pigmentation

Pigment on newly hatched larvae is scattered lightly on the head and snout, and appears on the dorsal, lateral, and ventral body surface above the abdominal cavity and also in the tail region. No pattern is obvious. The eyes are unpigmented.

In the head region, the eyes begin to darken by 4 d (about 3.8-4.0 mm) after hatching and are fully pigmented by 7 d (3.9-4.1 mm) in the reared larvae. Eyes in the smallest plankton specimen (2.9 mm) are pigmented. During early development, pigment over the head and snout disappears (by about 4 mm in reared larvae, 2.9 mm in planktonic larvae) except for a few internal melanophores above the otic capsule. Pigment appears on the lower jar and throat region by 4 or 5 mm and persists through the larval period. By about 6 or 7 mm several melanophores are present at the ventral angle of the preopercle. Later in development, scattered melanophores are added on the head (>10 mm) and on the upper jaw (>14 mm). Additional pigment is added to the entire head region on the eyed side during transformation (>17 mm).

In the abdominal region, melanophores disappear from the dorsal and lateral body surfaces above the gut cavity by the time larvae are about 4 mm long. Pigment is added again in this region during the transformation period when larvae are about 17 mm long. It is added first in two patches on the dorsal pterygiophores. More melanophores are then added laterally as well as on the dorsal pterygiophores, mainly along the myosepta, obscuring the original patches. A series of internal melanophores develops dorsal to the notochord above the abdominal cavity in larvae >10 mm. Melanophores are added along the ventral margin of the gut cavity by the time larvae are about 4 mm long. With development, additional melanophores extend over the ventral and posterior portions of the abdominal cavity appearing in a half-moon shape on most larvae >8 mm long. This pattern persists until transformation when the increase in body pigment on the eyed side obscures it.

In the tail region, three characteristic bands of pigment become obvious in reared larvae 4 d (3.9-4.1 mm) after hatching and are visible on the 2.9 mm plankton caught larvae. These are located on the body at positions roughly 50, 67, and 90% SL. In larvae <10 mm, these bands generally extend from dorsal to ventral body margins. With development the middle band becomes the most pronounced of the three. This middle band remains visible on the eyed side of some newly transformed benthic juveniles, and remnants of it persist on the blind side of juveniles as long as 35 mm. After notochord flexion (>14 mm), the posterior band is seen as a line of pigment at the base of the caudal fin. The anterior band becomes less pronounced and often does not extend above the lateral midline in larvae >14 mm. Along the notochord, a series of internal melanophores develops dorsal to

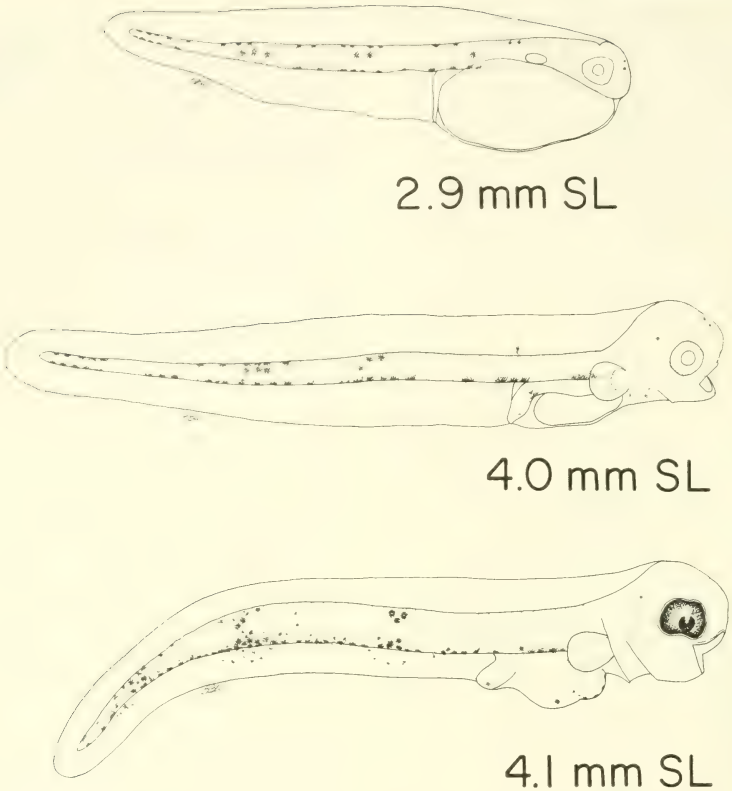


FIGURE 2.—*Isopsetta isolepis* larvae: 2.9 mm SL (reared, newly hatched, 144 h after fertilization); 4.0 mm SL (reared, 4 d after hatching); 4.1 mm SL (plankton specimen).

it, first in the region of the anterior two pigment bands in larvae about 6 or 7 mm long. Additional internal pigment spots then develop along the notochrod between the three pigment bands and anterior to them. This line of internal pigment spots is usually not continuous. It remains visible until the end of the transformation period. Along the ventral midline, pigment appears as a characteristic double row (viewed ventrally) of small melanophores in larvae >4 mm. This double row remains obvious until the onset of anal fin formation, about 14 mm, after which these melanophores appear to line the base of the anal fin, sometimes with one melanophore/fin ray. These melanophores become indistinct during transformation. On the ventrolateral body surface, melanophores are added just above the ventral midline row about the time the anal fin begins to form, around 10 mm. These melanophores eventually, by 12 mm, appear in the myosepta in a line midway between the lateral midline and the ventral margin of the body myomeres. Until the addition of pigment during transformation this line of melanophores is visible on the eyed side only, but is often visible on the blind side of newly transformed benthic juveniles. Along the margin of the ventral finfold a line of evenly spaced small melanophores is visible on newly preserved larvae >4 mm. This is often faded after a long period of preservation or is missing in plankton collected

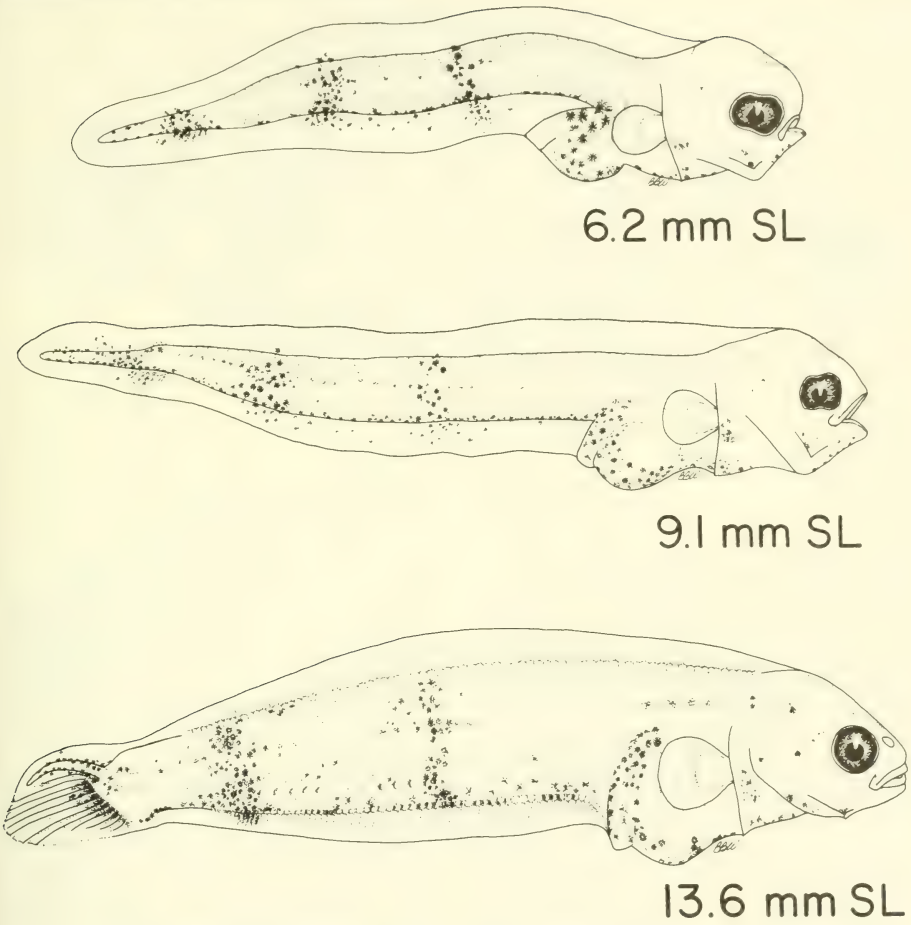


FIGURE 3.—*Isopsetta isolepis* larvae: 6.2 mm SL, 9.1 mm SL, and 13.6 mm SL.

specimens due to damaged finfolds. It is not visible on most specimens examined in this study, including the series illustrated. This line of melanophores has been seen on a few specimens up to 7.3 mm long. Additional pigment develops on the ventral finfold in the vicinity of the three pigment bands in larvae >4 mm and on the dorsal finfold near the posteriormost pigment band by the time larvae are 8 mm. This finfold pigment persists until caudal and anal fin formation. After the dorsal and anal fins are formed, by the time larvae are >15 mm, their margins are fringed with melanophores. However, the fin margins are often damaged on preserved planktonic specimens and the pigment fringing is not visible.

With transformation, at >17 mm, pigment is added to the eyed side in the tail region. Four or five clusters of melanophores appear along the dorsal pterygiophores and four along the ventral pterygiophores. These clusters eventually become obscured as more pigment is added. Increases in the number of melanophores along the bases of the

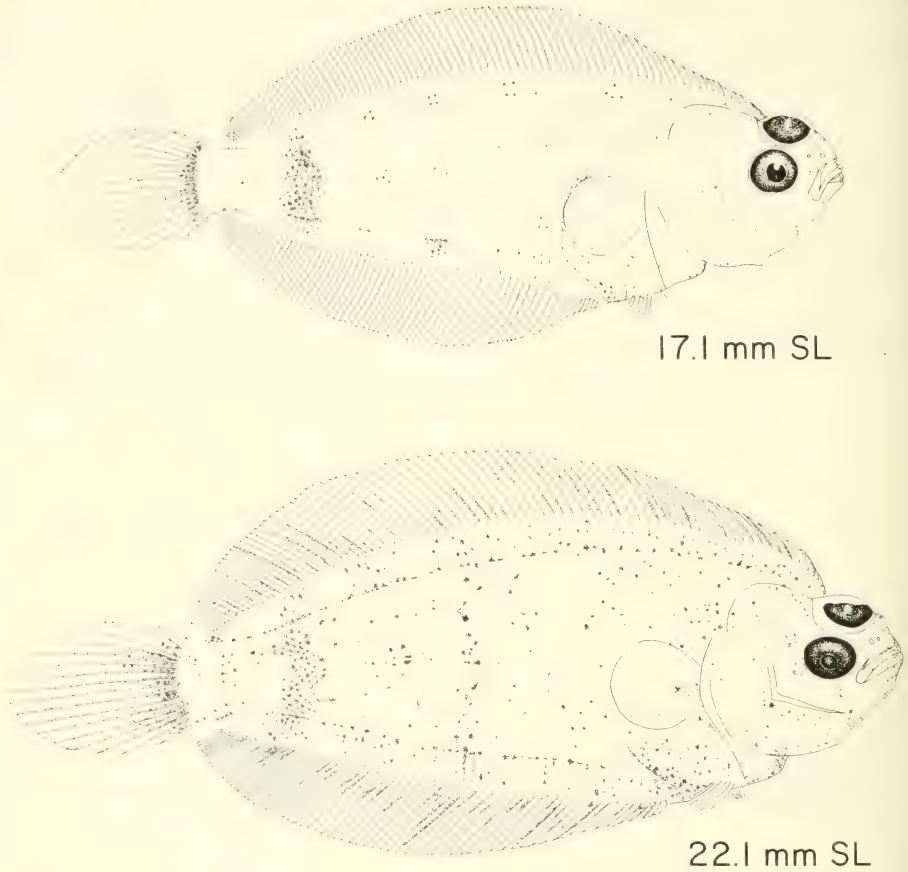


FIGURE 4.—*Isopsetta isolepis* larvae: 17.1 mm SL and 22.1 mm SL.

dorsal and anal pterygiophores give the appearance of solid lines of pigment. More melanophores appear on the body until all larval pigment is obscured. Additional pigment develops on the dorsal, anal, and caudal fins along the fin rays.

Morphology

Newly hatched reared larvae, 144 h after fertilization, range in length from 2.68 to 2.92 mm ($\bar{X}$ = 2.78 mm, based on 50 specimens). The yolk sac extends along the anterior third of the body. The mouth is not yet formed. A moderate finfold extends from the head around the posterior part of the body to the anus. The otic capsule is visible on the head behind the unpigmented eye. The mouth is formed by 2 d (3.4-3.5 mm) after hatching. The yolk is nearly gone by 4 d (3.8-4.0 mm) and is no longer visible by 7 d (3.9-4.1 mm). By 11 d (3.3-4.1 mm) the previously straight gut begins to coil. The smallest larva identified from plankton collections is 2.9 mm. It has a formed mouth, no remnant of yolk, and its gut has begun to coil. The size discrepancy may be an artifact of preservation, or it may

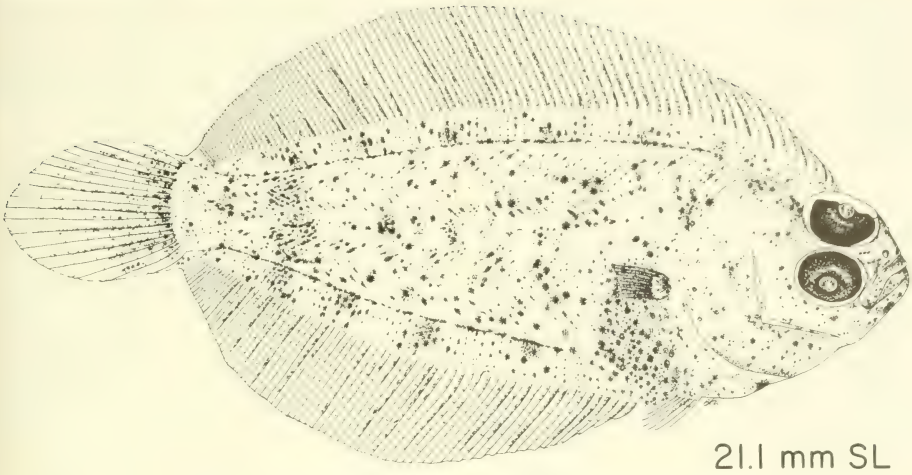


FIGURE 5.—Recently transformed benthic juvenile *Isopsetta isolepis*, 21.1 mm SL.

be due to the different environmental conditions of the reared and planktonic larvae. With development the gut continues to coil and the hindgut, which is initially directed posteriorly, comes to rest in an anteriorly directed position, by about 17 mm.

Notochord flexion begins by the time larvae are about 9 or 10 mm long and the notochord is fully flexed by about 14 mm. After flexion is complete, the tip of the urostyle continues to extend beyond the hypural plate, sometimes until larvae are 17 mm long. When larvae are about 12 or 13 mm long, near the end of notochord flexion, the left eye begins to migrate to the right side of the head. The left eye is visible on the ridge of the head, when viewed from the right side, in some larvae as small as 15 mm and consistently in specimens >17 mm. The left eye eventually migrates to the degree that it is directed upward, the most advanced position before complete transformation to benthic juvenile. This was the most advanced stage of eye migration of specimens taken in plankton tows and was observed in some, but not all, specimens >20 mm. The largest specimen collected in the plankton was 23.6 mm, but the most developed plankton specimen in terms of eye migration and increased pigmentation was 21.9 mm. The smallest specimen collected in a beam trawl was 18.0 mm, but its eye was on the dorsal ridge of the head directed upward and it had not completed transformation. The smallest benthic juvenile, in which the left eye had crossed over the middorsal ridge and juvenile pigment had intensified on the eyed side, was 18.5 mm.

With development (Tables 2, 3), relative head length increases considerably from mean values of 13-15% SL in preflexion larvae to 25% SL in postflexion larvae. Snout to anus length remains essentially constant with respect to standard length with mean values of 29-32%. Relative body depths at the pectoral fin base, at the anus, and behind the anus increase dramatically through the larval period with mean values nearly doubling in most cases between preflexion and flexion stages and doubling again between flexion and postflexion stages. The greatest rate of increase occurs in the depth behind the anus. Depth of the caudal peduncle also increases from 3 to 10% relative to standard length. Relative eye diameter is largest in preflexion larvae (29-36% HL (head length)) and decreases in flexion (24% HL) and postflexion (22% HL) larvae as does the relative length of the upper jaw (37-25% HL).

Ossification of Meristic Structures

Descriptions, based on cleared and stained specimens, depict only general trends of development because the size at which bones begin to ossify may vary among specimens and the uptake

TABLE 2.—Measurements (millimeters) of plankton caught larvae of *Isopsetta isolepis*. (Specimens between dashed lines are undergoing notochord flexion.)

Length interval (mm)	Sample size (*N*)	Mean length (mm)	Snout to anus	Head length	Snout length	Upper jaw length	Eye diameter	Body depth at pectoral fin base	Depth at anus	Depth behind anus	Caudal peduncle depth
2.9-3.0	2	2.90	0.95	0.45	—	—	0.20	0.30	0.20	0.15	0.10
3.1-4.0	[1]6	3.67	1.07	0.50	0.10	—	0.20	0.40	0.30	0.17	0.10
4.1-5.0	[2]4	4.63	1.28	0.55	0.10	—	0.25	0.40	0.35	0.23	0.10
5.1-6.0	[3]5	5.50	1.48	0.68	0.10	0.30	0.28	0.50	0.46	0.22	0.10
6.1-7.0	[4]5	6.58	2.04	1.02	0.12	0.40	0.30	0.72	0.72	0.34	0.12
7.1-8.0	[5]5	7.76	2.20	1.14	0.10	0.43	0.32	1.04	1.00	0.44	0.16
8.1-9.0	6	8.77	2.58	1.32	0.10	0.48	0.38	1.17	1.12	0.50	0.28
9.1-10.0	4	9.68	2.88	1.48	0.20	0.50	0.45	1.25	1.23	0.60	0.35
10.1-11.0	6	10.57	3.42	1.95	0.28	0.62	0.48	1.72	1.68	1.25	0.60
11.1-12.0	4	11.25	3.38	1.88	0.20	0.60	0.50	1.78	1.72	1.15	0.55
12.1-13.0	5	12.36	3.70	2.24	0.28	0.76	0.50	2.02	2.14	1.54	0.74
13.1-14.0	5	13.55	4.22	2.74	0.36	0.72	0.62	2.52	3.12	2.08	0.96
14.1-15.0	5	14.48	4.84	3.18	0.50	0.86	0.64	3.18	3.68	3.00	1.34
15.1-16.0	5	15.38	4.68	3.58	0.54	0.94	0.74	3.74	4.40	3.64	1.48
16.1-17.0	5	16.54	5.64	4.00	0.60	1.10	0.90	4.64	5.36	4.84	1.68
17.1-18.0	5	17.50	5.88	4.70	0.78	1.12	1.10	5.60	6.16	6.00	1.86
18.1-19.0	4	18.63	5.85	4.78	0.93	1.28	1.08	6.43	6.85	6.95	1.88
19.1-20.0	6	19.55	5.92	4.93	0.94	1.20	1.08	6.52	7.00	6.90	2.02
20.1-21.0	6	20.53	5.97	5.12	0.95	1.28	1.10	6.90	7.35	7.50	2.03
21.1-22.0	4	21.48	6.40	5.93	0.95	1.60	1.23	7.68	8.18	8.58	2.23
22.1-23.0	6	22.48	6.27	5.58	0.95	1.22	1.23	7.67	8.33	8.62	2.28
23.1-24.0	4	23.33	6.80	5.68	0.98	1.43	1.25	7.83	8.48	9.03	2.33

[1]*N* = 2 for snout length.
[2]*N* = 3 for snout length.
[3]*N* = 4 for snout length and 1 for upper jaw length.
[4]*N* = 1 for upper jaw length.
[5]*N* = 4 for upper jaw length.

TABLE 3.—Body proportions of *Isopsetta isolepis* larvae. Values given are percentages: mean ± standard deviation, and range in parentheses.

Item	Preflexion larvae with yolk (reared)	Preflexion larvae without yolk (reared)	Preflexion larvae without yolk (plankton)	Flexion larvae (plankton)	Postflexion larvae (plankton)
No. measured	20	42	[1]37	[2]20	50
SL	(2.7-4.0)	(3.4-5.4)	(2.9-9.0)	(10.5-14.2)	(13.5-23.6)
Head length/SL	15.0±2.7(10.6-19.6)	13.4±0.9(11.3-15.9)	14.2±2.0(10.2-17.2)	18.3±1.6(15.3-20.7)	24.9±2.1(20.7-29.4)
Snout to anus length/SL	32.4±3.8(28.3-39.3)	28.8±1.3(26.7-31.1)	29.2±2.9(22.9-34.4)	30.7±1.8(27.6-34.0)	31.0±3.0(23.2-35.8)
Depth at pectoral fins/SL	5.2±0.8(4.1-6.7)	9.2±1.0(7.4-11.6)	11.4±2.3(8.3-15.2)	16.6±1.7(12.9-18.5)	31.1±5.0(20.1-38.0)
Depth at anus/SL	9.8±1.2(8.2-12.0)	8.9±0.9(6.9-11.1)	10.3±2.8(5.7-15.6)	17.8±3.7(12.9-28.9)	34.1±4.4(23.2-40.2)
Depth behind anus/SL	4.3±0.7(2.8-5.9)	3.2±0.5(2.5-4.1)	5.1±1.3(2.9-7.8)	12.3±2.0(9.0-14.8)	33.4±6.7(18.8-41.3)
Caudal peduncle depth/SL	—	—	2.6±0.8(1.3-4.1)	6.0±1.1(4.4-7.4)	9.6±2.0(7.6-11.3)
Eye diameter/HL	32.8±2.6(30.2-38.1)	28.9±3.9(21.6-39.6)	35.6±9.1(25.0-50.0)	23.7±2.8(20.0-29.4)	21.8±2.2(17.5-26.2)
Snout length/HL	19.9±6.0(9.4-29.8)	28.1±4.1(20.8-34.0)	12.5±4.4(6.7-20.0)	13.7±2.8(8.7-21.0)	16.6±3.7(9.4-20.8)
Upper jaw length/HL	—	—	37.1±4.9(31.2-50.0)	31.6±5.9(24.0-47.6)	25.2±4.4(17.5-38.5)

[1]Except *N* = 29 for snout length and *N* = 16 for upper jaw length.
[2]Except *N* = 19 for snout length.

of stain may be affected by length of preservation. Terminology of bones generally follows Richardson and Joseph (1973) and Frame et al. (1978) except as noted.

Most of the meristic characters of *I. isolepis* larvae begin ossifying during notochord flexion (10-14 mm); only gill rakers and pectoral fin rays begin to ossify at larger sizes (Table 4; Figure 6). The following discussion roughly parallels the sequence of development of meristic characters, and we note their first appearance as well as the onset of ossification as indicated by the acceptance of Alizarin Red stain.

Paired conical teeth may be observed on the dentary of 5.3 mm larvae, and on the premaxillaries by 5.8 mm. Teeth continue to increase in number as the larvae grow. Teeth are consistently more numerous on the left (ultimately the blind) side of the head than the right side. The smallest specimen in which teeth accepted alizarin stain was 12 mm, possibly an artifact of preservation. Larval teeth develop in approximately two nonparallel rows. The outer row consists of conical, caninelike teeth, and the inner row is composed of smaller, curved teeth. Most teeth are ossified in 18 mm larvae. By transformation (ca. 20.0 mm), butter sole larvae possess approximately 37 larval teeth on the left dentary (27 in the outer row; 10 smaller teeth on an inner row) and about 37 large conical teeth on the left premaxillary arranged in

TABLE 4.—Development of meristic structures in *Isopsetta isolepis* larvae. Mean data are given for larvae in the specified length range. (Specimens between dashed lines are undergoing notochord flexion.)

SL (mm)	Sample size	Dorsal fin rays	Anal fin rays	Caudal fin rays	Pectoral fin rays		Pelvic fin rays		Neural spines			Haemal spines	Centra			Branchiostegal rays	Gill rakers	
					Left	Right	Left	Right	Abdom.	Caudal	Total		Abdom.	Caudal	Total		Upper	Lower
3.2-8.9	50	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
9.0-9.9	5	—	—	1.8	—	—	—	—	—	—	—	—	—	—	—	0.8	—	—
10.0-10.9	12	—	—	4.4	—	—	—	—	2.0	9.2	11.2	9.2	—	—	—	1.8	—	—
11.0-11.9	12	11.6	9.2	10.7	—	—	0.3	0.3	5.7	20.8	26.5	20.8	0.8	2.8	3.6	5.0	—	—
12.0-12.9	15	19.6	17.2	14.9	—	—	—	—	8.9	26.7	35.6	26.5	0.3	4.2	4.3	6.0	—	—
13.0-13.9	17	51.8	34.8	15.5	—	—	0.9	0.9	8.1	27.5	35.6	27.5	3.5	16.3	19.8	5.9	—	—
14.0-14.9	18	45.0	36.8	14.6	—	—	0.4	0.4	9.1	27.1	36.2	27.0	4.9	19.0	23.9	6.1	—	—
15.0-15.9	17	52.9	46.8	15.4	—	—	2.2	2.2	8.2	24.8	33.0	24.8	6.4	22.0	28.6	5.6	—	—
16.0-16.9	10	72.2	55.0	18.0	—	—	2.1	2.1	9.9	30.5	40.4	30.5	9.9	31.8	41.7	7.0	—	—
17.0-17.9	11	89.7	67.5	18.0	0.5	0.5	4.5	4.5	10.0	31.2	41.2	31.2	10.0	32.2	42.2	7.0	—	—
18.0-18.9	15	87.3	66.9	18.0	0.7	0.7	5.0	5.0	9.9	30.9	40.8	30.9	9.9	31.9	41.7	7.0	—	0.3
19.0-19.9	9	87.9	67.9	18.0	0.3	0.3	6.0	6.0	9.9	31.2	41.1	31.0	9.9	32.0	41.9	7.0	—	—
20.0-20.9	9	88.0	68.1	18.0	1.8	1.8	6.0	6.0	9.9	30.9	40.8	30.8	9.9	31.7	41.6	7.0	—	1.7
21.0-21.9	4	88.8	67.8	18.0	2.3	2.3	6.0	6.0	10.0	30.8	40.8	30.8	10.0	31.8	41.8	7.0	—	1.0
22.0-22.9	5	91.2	68.8	18.0	5.0	5.0	6.0	6.0	10.0	31.0	41.0	30.8	10.0	31.8	41.8	7.0	—	2.8

two rows. The right dentary contains about 20 teeth (11 large conical teeth in the outer row and 9 smaller teeth in the inner row). The right premaxillary contains nine larger teeth and six smaller teeth. Teeth continue to increase in number after transformation. A 44 mm juvenile possessed about 40 teeth each on the left premaxillary and left dentary and 14 teeth on the right dentary and 10 teeth on the right premaxillary.

Neural spines ossify during notochord flexion (Table 4; Figure 6). The first neural spine to ossify lies just above the first haemal spine in the anterior abdominal region, and ossification proceeds posteriorly and anteriorly. The last two neural spines to ossify are those on the antepenultimate and penultimate vertebrae. Ossification is usually completed at about 16.5 mm. Haemal spines ossify from anterior to posterior beginning with the first haemal spine. The last two haemal spines to ossify are also on the antepenultimate and penultimate vertebrae.

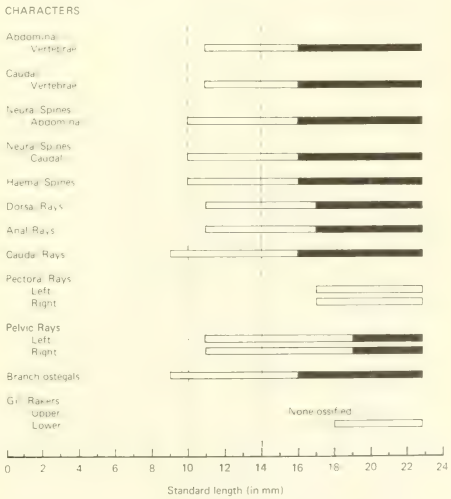


FIGURE 6.—Diagrammatic summary of the sequence of ossification of principal meristic structures in *Isopsetta isolepis*. Dashed vertical lines indicate size range in which notochord flexion occurs; open bars indicate meristic structure is undergoing ossification; solid bars indicate meristic structure is completely ossified.

In the axial skeleton the first centrum to ossify (as early as 11 mm) supports the first haemal spine. Ossification proceeds both anteriorly and posteriorly, with the urostyle ossifying before the antepenultimate and penultimate vertebrae. All centra are ossified by 17 mm.

The first caudal supports to ossify are hypurals[10] 2 and 3 in larvae as small as 12 mm. Hypural 1 is ossified by 13 mm and hypural 4 at about 15 mm. The epurals ossify last at about 16 mm. We interpret the caudal complex of *I. isolepis* to consist of four hypurals (two below and two above the medial axis) and two epurals. One is a normal-sized epural that supports the uppermost caudal ray, and the other epurallike bone is reduced in size and supports no rays (Figure 6H). No uroneurals are present.

Fin rays begin to ossify during notochord flexion (10-14 mm) in the dorsal, anal, caudal, and pelvic fins. Ossification is completed in the following order: caudal, dorsal, anal, pelvic, and pectoral fins (Table 4; Figure 6). Pectoral fin rays were not fully ossified in the largest stained larva, 22.8 mm.

The anlage of the base of the caudal fin begins to form by 5.5 mm (Figure 7A). Incipient caudal rays are evident from 5.5 to 8.8 mm. By 10.5 mm (Figure 7 B) the notochord begins to flex and hypurals 1-3 develop, supporting about eight incipient rays. At about 12.7 mm the notochord is usually fully flexed and three hypurals are evident, supporting 10 differentiated but unossified caudal rays (Figure 7C). By 14.3 mm (Figure 7D), hypurals 1-3 are ossified and some caudal rays have started ossifying, beginning at the center of the fin and proceeding dorsally and ventrally. The full complement of 18 rays is consistently ossified by 16.4 mm (Figure 7E). By 18.0 mm (Figure 7F) all four hypurals and both epurals are ossified. By 22.8 mm (Figure 7G) the caudal fin essentially resembles that of a juvenile (Figure 7H) and nearly all elements of the caudal complex are ossified. The 18 rays, consisting of (from ventral to dorsal) 3 unbranched rays, 12 branched rays, and 3 unbranched rays, are carried on the hypurals as follows: epural 1, 1 ray; hypural 4, 2 rays; hypural 3, 6 rays; hypural 2, 5 rays; hypural 1, 4 rays.

Incipient dorsal fin rays may be observed in the proximal portion of the finfold at midbody by 10.5 mm. Ossification of dorsal rays begins at midbody by 11 mm and proceeds anteriorly and posteriorly. By 17.5 mm the dorsal rays reach their full complement and are completely ossified.

The anal fin develops in a manner analagous to the dorsal fin and nearly simultaneously. Rays begin to differentiate at midbody with formation progressing both anteriorly and posteriorly. Ossified rays begin at midbody at about 11 mm and the full complement may be ossified by 17.5 mm.

Pelvic fin buds may be observed on larvae as small as 10 mm, although not consistently until notochord flexion is complete at about 14 mm, and individual rays may begin ossifying by 11 mm. The full complement of six rays is ossified by 19 mm.

Pectoral fin buds are visible above the yolk sac in newly hatched reared larvae. Larval pectoral fins are present in the smallest stained larvae examined (3.2 mm). The rays begin to differentiate by 13.5 mm and individual rays begin ossifying as transformation occurs by about 17 mm. The full complement of pectoral rays was not attained in the largest larva examined, 22.8 mm, but is fully developed in a 44 mm juvenile.

Branchiostegal rays begin to accept alizarin stain at about 9.5 mm. The adult complement of seven rays may be differentiated, but not ossified, by 13.6 mm. All rays are ossified by 16 mm.

Gill rakers on the first ceratobranchial begin forming at about 7 mm. A maximum of six rakers was formed in the largest stained larva examined (22.8 mm). No rakers were formed on the epibranchials of this specimen. The adult complement of four plus seven gill rakers is present on a 44 mm juvenile.

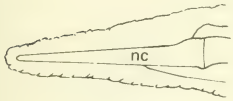
Of the median fin supports, pterygiophores supporting anal and dorsal fin rays begin ossifying at about 19 mm. These pterygiophores are completely ossified by 22.8 mm (Figure 8).

Scales form sometime between 22.8 mm (largest stained larva) and 44 mm (smallest stained juvenile).

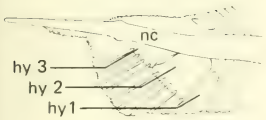
OCCURRENCE

Off Oregon, larvae of *I. isolepis* are distributed mainly in the near coastal zone within 18 km of shore, with abundance peaks at 6-9 km (Richardson 1973, see footnote 4; Richardson and Pearcy 1977). Smaller numbers of larvae have been taken as far as 56 km offshore (Richardson and Pearcy 1977; Laroche and Richardson 1979), inside the mouth of Yaquina Bay (Pearcy and

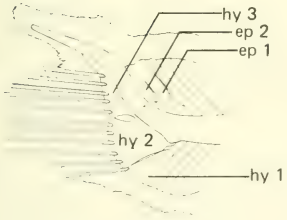
[10]We follow Moser and Ahlstrom's (1970) definition of hypurals "... all bones of hypaxial origin associated with ural centra [are defined] as hypurals, including the lowermost bone."



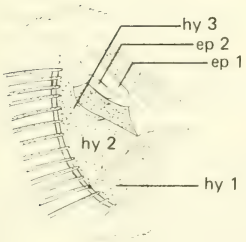
A 5.5mm



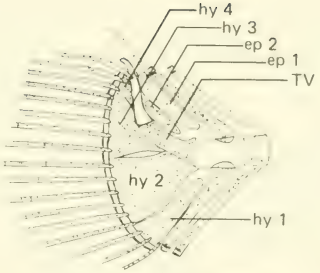
B 10.5mm



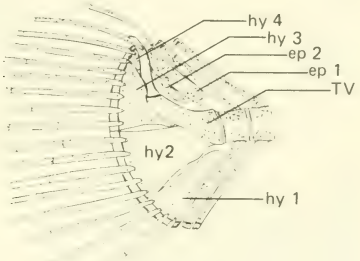
C 12.7mm



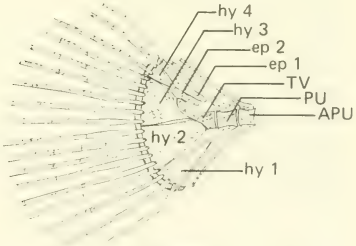
D 14.3mm



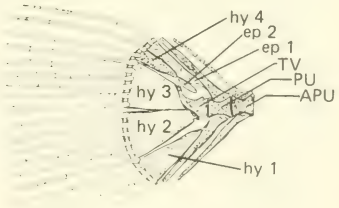
E 16.4mm



F 18.0mm



G 22.8mm



H 44.0mm

FIGURE 7.—Development of the caudal fin of *Isopsetta isolepis*: 5.5 mm SL, 10.5 mm SL, 12.7 mm SL, 14.3 mm SL, 16.4 mm SL, 18.0 mm SL, 22.8 mm SL, and 44.0 mm SL. Ossified elements are stippled. hy = hypurals; ep = epurals; nc = notochord; APU = antepenultimate vertebrae; PU = penultimate vertebrae; TV = terminal vertebrae.

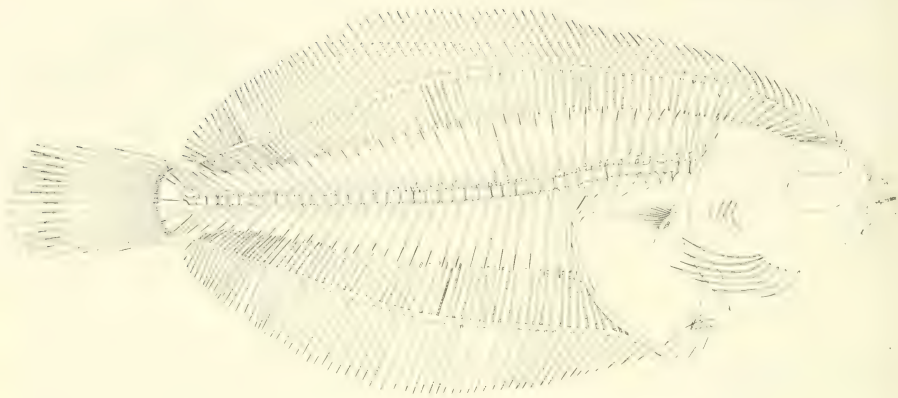


FIGURE 8.—Juvenile *Isopsetta isolepis*, 44 mm SL, showing details of skeletal structure.

Myers 1974), and in the Columbia River (Misitano 1977). A similar coastal distribution is indicated off Washington with reduced numbers occurring in Puget Sound (Waldron 1972; Blackburn 1973). Thus spawning takes place primarily in coastal areas rather than bays and estuaries.

Larvae occur in the plankton off Oregon mainly in winter and spring (Waldron 1972; Misitano 1977; Richardson see footnote 4) although in 1971 larvae were taken in every month of the year except September, November, and December (Richardson see footnote 4). In 1972 they were taken in every month sampled, March through August (Richardson see footnote 4). In 1971, abundance peaked in May, and in 1972, smaller abundance peaks were observed in March and May (Richardson see footnote 4). Spring occurrences of larvae have been reported off Washington and in Puget Sound (Waldron 1972; Blackburn 1973).

Monthly length-frequency distributions and median lengths of larvae collected off Oregon indicate winter-spring spawning (Figure 9). Small larvae <5 mm were taken January through May 1971, October 1971, and March and April 1972. Median lengths increased progressively from 2 to 16 mm in January through June 1971 and from 4 to 16 mm in March through June 1972.

Based on available data, *I. isolepis* apparently settles to the bottom in coastal areas and remains near the coast during the early juvenile period. Newly transformed juveniles (18-38 mm) have been collected off the mouth of the Columbia River in depths of 34-56 m (Table 5). Juveniles in this size range have not been reported from bays, estuaries, and nearshore coastal areas where juvenile *Parophrys vetulus* have been found (Westrheim 1955; Kendall 1966; Beardsley 1969; William Johnson's data listed in Pearcy and Myers 1974; Peden and Wilson 1976; Laroche and Holton 1979; Cummings and Schwartz[11]; Higley and Holton[12]; Krygier[13]). Although Misitano (1977) reported that both *I. isolepis* and *P. vetulus* use the Columbia River as a nursery area, he was referring to fish >85 mm long (>95 mm for *I. isolepis*). Thus, smaller *I. isolepis* juveniles apparently use offshore coastal areas during their first year of life as opposed to the bay, estuarine, and near coastal nursery habitats of *P. vetulus*.

TABLE 5.—Data from beam trawl collections of juvenile *Isopsetta isolepis* taken off the mouth of the Columbia River, 1975.

Date	Location (Lat. N, long. W)	Depth (m)	Specimens (no.)	SL of larvae	
				Median (mm)	Range (mm)
26 June	46°11.5′, 124°07.6′	37	86	24	18-38
26 June	46°09.5′, 124°06.3′	40	7	21	18-24
14 Sept.	46°09.5′, 124°05.0′	34	5	24	22-26
15 Sept.	46°09.3′, 124°08.0′	56	11	25	20-28

[11]Cummings, E., and E. Schwartz. 1971. Fish in Coos Bay, Oregon, with comments on distribution, temperature, and salinity of the estuary. Oreg. Fish Comm., Res. Div., Coastal Rivers Invest. Inf. Rep. 70-11, 22 p.

[12]Higley, D. L., and R. L. Holton. 1975. Biological baseline data, Youngs Bay, Oregon, 1974. Final Rep. Alumex Pacific Aluminum Corp., 1 November 1973 through 30 April 1975. Oreg. State Univ., Sch. Oceanogr. Ref. 75-6, 91 p.

[13]E. Krygier, Research Assistant, School of Oceanography, Oregon State University, Corvallis, OR 97331, pers. commun. June 1978.

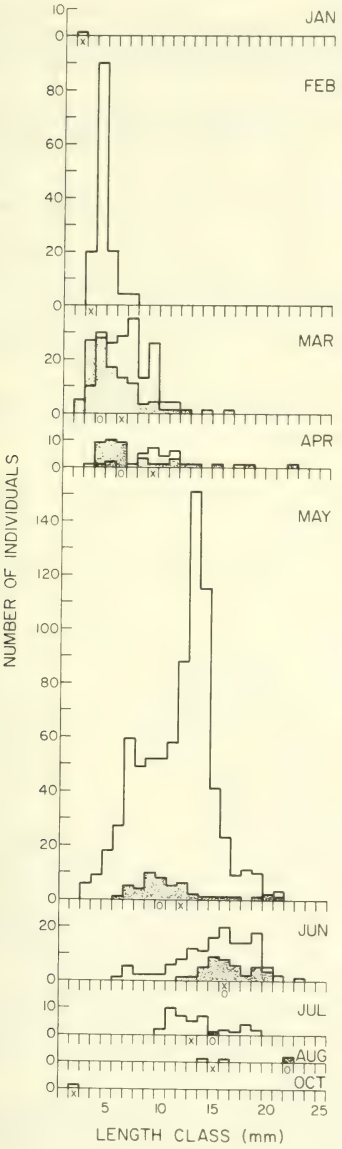


FIGURE 9.—Length-frequency histograms of *Isopsetta isolepis* larvae collected in 70 cm bongo nets off Oregon in 1971 (unshaded) and 1972 (shaded). X = median length of larvae in 1971; 0 = median length of larvae in 1972.

The habitat separation of newly transformed benthic juveniles of *I. isolepis* and *P. vetulus* is interesting since spawning times overlap for the two species and the larvae are codominants in coastal waters off Oregon (Richardson and Pearcy 1977). Habitat separation also has been noted in large (>10 mm) larvae; *P. vetulus* is more abundant in neuston samples relative to plankton samples than *I. isopsetta* (Laroche and Richardson 1979). Ratios of relative abundance of *P. vetulus* to *I. isolepis* in plankton samples was 2:1 compared with 36:1 in neuston samples. Thus the two cooccurring species appear to be utilizing different parts of the water column. Smaller larvae might be segregated similarly by depth, but we have no data on vertical distribution to substantiate this idea. Feeding studies, which may help verify these habitat differences and provide evidence for resource partitioning between these morphologically similar larvae, remain to be conducted.

ACKNOWLEDGMENTS

We thank Michael D. Richardson (Department of Navy, NORDA; formerly OSU) for providing juvenile specimens from beam trawl collections off the mouth of the Columbia River. Betsy Washington (OSU) illustrated the larvae and juvenile; Beverly Vinter (NWAFC) illustrated the caudal fin and skeleton; Kenneth Waldron (NWAFC) reared the *I. isolepis* eggs. Elbert H. Ahlstrom (Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla, Calif.) provided unpublished meristic data on *I. isolepis*; he also provided stimulating discussions on osteology of pleuronectids. Earl Krygier (OSU) provided information on juvenile flatfishes collected in Yaquina Bay and Oregon coastal waters. Gail Gibbard (formerly OSU) compiled the morphometric data. We thank Beverly Vinter, Ann Matarese, and Kenneth Waldron for technical assistance.

This work is a result, in part, of research sponsored by the Oregon State University Sea Grant College Program, supported by NOAA Office of Sea Grant, Department of Commerce, under Grant No. 04-6-158-44094.

LITERATURE CITED

AHLSTROM, E. H., AND R. C. COUNTS.
1955. Eggs and larvae of the Pacific hake, *Merluccius productus*. U.S. Fish. Wildl. Serv., Fish. Bull. 56:295-329.

AHLSTROM, E. H., AND H. G. MOSER.
1975. Distributional atlas of fish larvae in the California Current region: Flatfishes, 1955 through 1960. Calif. Coop. Oceanic. Fish. Invest. Atlas 23, 207 p.

ALDERDICE, D. F., AND C. R. FORRESTER.
1971. Effects of salinity and temperature on embryonic development of the petrale sole (*Eopsetta jordani*). J. Fish. Res. Board Can. 28:727-744.
1974. Early development and distribution of the flathead sole (*Hippoglossoides elassodon*). J. Fish. Res. Board Can. 31:1899-1918.

BEARDSLEY, A. J.
1969. Movement and angler use of four foodfishes in Yaquina Bay, Oregon. M.S. Thesis, Oregon State Univ., Corvallis, 173 p.

BLACKBURN, J. E.
1973. A survey of the abundance, distribution and factors affecting distribution of ichthyoplankton in Skagit Bay. M.S. Thesis, Univ. Washington, Seattle, 136 p.

BUDD, P. L.
1940. Development of the eggs and early larvae of six California fishes. Calif. Div. Fish Game, Fish Bull. 56, 50 p.

DEKHNIK, T. V.
1959. Materialy po Razmnozhenyv i Rasvitiyu Nekotorykh Dal Nevostochnykh Kambal. [Material on spawning and development of certain far eastern flatfishes.] [In Russ.] Issled. Dal'Nevost. Morei SSSR, Tr. Kuriol-Sakhalin. Eksped. 6(2):111-131.

DEMORY, R. L.
1971. Depth distribution of some small flatfishes off the northern Oregon-southern Washington coast. Res. Rep. Fish Comm. Oreg. 3:44-48.

DINGERKUS, G., AND L. D. UHLER.
1977. Enzyme clearing of alcian blue stained whole small vertebrates for demonstration of cartilage. Stain Technol. 52:229-232.

FRAME, D. W., T. J. ANDREWS, AND C. F. COLE.
1978. Osteology of the American plaice, *Hippoglossoides platessoides*. Postilla 173, 32 p.

HAGERMAN, F. B.
1952. The biology of the Dover sole, *Microstomus pacificus* (Lockington). Calif. Dep. Fish Game, Fish Bull. 85, 48 p.

HART, J. L.
1973. Pacific fishes of Canada. Fish. Res. Board Can., Bull. 180, 740 p.

HICKMAN, C. P., JR.
1959. The larval development of the sand sole (*Psettichthys melanostictus*). Wash. Dep. Fish., Fish Res. Pap. 2(2):38-47.

KENDALL, A. W., JR.
1966. Sampling juvenile fishes on some sandy beaches of Puget Sound, Washington. M.S. Thesis, Univ. Washington, Seattle, 77 p.

LAROCHE, J. L., AND S. L. RICHARDSON.
1979. Winter-spring abundance of larval English sole, *Parophrys vetulus*, between the Columbia River and Cape Blanco, Oregon during 1972-1975 with notes on occurrences of three other pleuronectids. Estuarine Coastal Mar. Sci. 8:455-476.

LAROCHE, W. A., AND R. L. HOLTON.
1979. Occurrence of 0-age English sole, *Parophrys vetulus*, along the Oregon coast: an open coast nursery area? Northwest Sci. 53:94-96.

LEVINGS, C. D.
1968. Fertilized eggs of the butter sole *Isopsetta isolepis*, in Skidegate Inlet, British Columbia. J. Fish. Res. Board Can. 25:1743-1744.

MILLER, B. S.
1969. Life history observations on normal and tumor-bearing flathead sole in East Sound, Orcas Island (Washington). Ph.D. Thesis, Univ. Washington, Seattle, 131 p.

MILLER, D. J., AND R. N. LEA.
1972. Guide to the coastal marine fishes of California. Calif. Dep. Fish Game, Fish Bull. 157, 235 p.

MISITANO, D. A.
1976. Size and stage of development of larval English sole, *Parophrys vetulus*, at time of entry into Humboldt Bay. Calif. Fish Game 62:93-98.
1977. Species compostion and relative abundance of larval and post-larval fishes in the Columbia River estuary, 1973. Fish. Bull., U.S. 75:218-222.

MOSER, H. G., AND E. H. AHLSTROM.
1970. Development of lanternfishes (family Myctophidae) in the California Current. Part I. Species with narrow-eyed larvae. Bull. Los Ang. Cty. Mus. Nat. Hist. Sci. 7, 145 p.

NAPLIN, N. A., AND C. L. OBENCHAIN.
In press. A description of eggs and larvae of the snake eel, *Pisodonophis cruentifer* (Ophichthidae). Bull. Mar. Sci. 30(2).

ORCUTT, H. G.
1950. The life history of the starry flounder, *Platichthys stellatus* (Pallas). Calif. Div. Fish Game, Fish Bull. 78, 64 p.

ORSI, J. J.
1968. The embryology of the English sole, *Parophrys vetulus*. Calif. Fish Game 54:133-155.

PEARCY, W. G., AND S. S. MYERS.
1974. Larval fishes of Yaquina Bay, Oregon: A nursery ground for marine fishes? Fish. Bull., U.S. 72:201-213.

PEDEN, A. E., AND D. E. WILSON.
1976. Distribution of intertidal and subtidal fishes of northern British Columbia and southeastern Alaska. Syesis 9:221-248.

PERTSEVA-OSTROUMOVA, T. A.
1960. Razmnozhenie i razvitie strelozubykh paltusov roda *Atheresthes* Jordan et Gilbert (Pleuronectidae Pisces). [The reproduction and development of the species of the genus *Atheresthes* Jordan and Gilbert (Pleuronectidae, Pisces).] [In Russ., Engl. summ.] Zool. Zh. 39:1659-1669. (Translated by S. Pearson, 1972, 17 p.; Northwest and Alaska Fisheries Center, NMFS, NOAA, Seattle, Wash.)
1961. Razmnozheni i razvitie dal'nevostochnykh kambal. [The reproduction and development of far-eastern flounders.] [In Russ.] Akad. Nauk SSSR, Inst. Okeanol., 484 p. (Transl. available as Fish. Res. Board Can., Transl. Ser. 856.)

RICHARDSON, S. L.
1973. Abundance and distribution of larval fishes in waters off Oregon, May-October 1969, with special emphasis on the northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 71:697-711.
In press. Pelagic eggs and larvae of the deepsea sole, *Embassichthys bathybius* (Pisces: Pleuronectidae), with comments on generic affinities. Fish. Bull., U.S. 79(1).

RICHARDSON, S. L., AND E. B. JOSEPH.
1973. Larvae and young of western North Atlantic bothid flatfishes *Etropus microstomus* and *Citharichthys arctifrons* in the Chesapeake Bight. Fish. Bull., U.S. 71: 735-767.

RICHARDSON, S. L., AND W. G. PEARCY.
1977. Coastal and oceanic fish larvae in an area of upwelling off Yaquina Bay, Oregon. Fish. Bull., U.S. 75: 125-145.

SOMMANI, P.
1969. Growth and development of sand sole postlarvae (*Psettichthys melanostictus*). M.S. Thesis, Univ. Washington, Seattle, 60 p.

SUMIDA, B. Y., E. H. AHLSTROM, AND H. G. MOSER.
1979. Early development of seven flatfishes of the eastern North Pacific with heavily pigmented larvae (Pisces, Pleuronectiformes). Fish. Bull., U.S. 77:105-145.

TAYLOR, W. R.
1967. An enzyme method of clearing and staining small vertebrates. Proc. U.S. Natl. Mus. 122, 17 p.

THOMPSON, W. F., AND R. VAN CLEVE.
1936. Life history of the Pacific halibut. 2. Distribution and early life history. Rep. Int. [Pac. Halibut] Fish. Comm. 9, 184 p.

WALDRON, K. D.
1972. Fish larvae collected from the northeastern Pacific Ocean and Puget Sound during April and May 1967. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-663, 16 p.

WESTRHEIM, S. J.
1955. Size composition, growth, and seasonal abundance of juvenile English sole (*Parophrys vetulus*) in Yaquina Bay. Res. Briefs Fish Comm. Oreg. 6(2):4-9.

YUSA, T.
1957. Eggs and larvae of flatfishes in the coastal waters of Hokkaido. I. Embryonic development of the starry flounder *Platichthys stellatus* (Pallas). Bull. Hokkaido Reg. Fish. Res. Lab. 15:1-14.

RETENTION OF THREE TAXA OF POSTLARVAL FISHES IN AN INTENSIVELY FLUSHED TIDAL ESTUARY, CAPE FEAR RIVER, NORTH CAROLINA

MICHAEL P. WEINSTEIN,[1] SIDNEY L. WEISS,[2] RONALD G. HODSON,[3] AND LAWRENCE R. GERRY[3]

ABSTRACT

Fixed nets were used to sample postlarvae of spot, *Leiostomus xanthurus*, Atlantic croaker, *Micropogonias undulatus*, and flounders, *Paralichthys* spp., over several 24-hour periods in the Cape Fear River, near Wilmington, North Carolina. Results of analyses of variance on abundance data collected at two locations indicate that these taxa exhibit distinct behavioral responses, primarily to photoperiod and tide, which allow them to maintain a selected position in the estuary and avoid being flushed seaward. The level of response to these variables dictates ultimate residence in at least two primary nurseries, the river main stem in the vicinity of the salt boundary and the tidal salt marshes. By migrating to the surface at night, both spot and flounders make apparent use of tides to augment lateral migration into marshes. Conversely, by tending to remain more bottom oriented at all times, Atlantic croaker accumulate in greater numbers in deep water at the head of the estuary.

Mechanisms by which larval fishes are recruited to, and concentrated in, estuaries are poorly understood. Attempts to elucidate these mechanisms suffered from the generally high degree of variability associated with sampling larval fish populations. Recognizing this, Graham (1972) employed fixed nets to collect larval Atlantic herring, *Clupea harengus*, in the Sheepscot estuary of Maine. His gear offered the advantage of obtaining synoptic samples over the entire water column, and because much greater volumes were filtered, the variability of the data was also reduced. Consequently, he was able to infer a mechanism used by Atlantic herring larvae to select a specific reach of the estuary, i.e., a behavioral response manifested by interactions between depth, or location, and tidal direction.

The importance of such interactions has not always been fully appreciated; e.g., Pearcy and Richards (1962) postulated that larval fish transport in the Mystic estuary occurred mainly in the lower layer by net nontidal flows. Similarly, Haven (1957) and Sandifer (1975) described utilization of net nontidal transport in the lower layers for fishes and invertebrates in the Chesapeake Bay. However, these investigators collected larvae during the daytime only and did not consider diel migrations which may bring many larvae to the surface at night (Pacheco and Grant 1968; Lewis and Wilkens 1971; Williams and Porter 1971). Moreover, certain larval fishes (e.g., menhaden) may also frequent the upper layers to a considerable extent during the day (Thayer et al. in press). Thus, it is probable that the retention mechanism is species-specific and involves several elements as described by Bousfield (1955): 1) diel changes in vertical distribution; 2) utilization of the residual, or nontidal, drift seaward in the upper layer and landward along the bottom; and 3) changing behavioral parameters with respect to tidal direction (e.g., see also Hughes 1969a, b, 1972; Turgeon 1976). Individual species may utilize one or more of these mechanisms to reach and stay within a preferred zone of the estuary, from its mouth (Carriker 1951) to the headwaters (Haven 1957; Turgeon 1976).

Here we describe distributions of postlarval fishes in two locations within the Cape Fear River estuary, near Southport, N.C. Both sampling areas were situated upriver, in an area believed to constitute a primary nursery zone for several fish species. Sampling was stratified by location, depth, photoperiod, and tidal direction, and an attempt was made to depict postlarval fish behavior with respect to these strata. A hypothesis is

[1]Lawler, Matusky & Skelly Engineers, One Blue Hill Plaza, Pearl River, N.Y.; present address: Department of Biology, Virginia Commonwealth University, Richmond, VA 23284.
[2]Lawler, Matusky & Skelly Engineers, One Blue Hill Plaza, Pearl River, N.Y.; present address: Sandoz, Inc., East Hanover, NJ 07936.
[3]Department of Zoology, North Carolina State University, Raleigh, NC 28603.

Manuscript accepted November 1979.
FISHERY BULLETIN: VOL. 78, NO. 2, 1980.

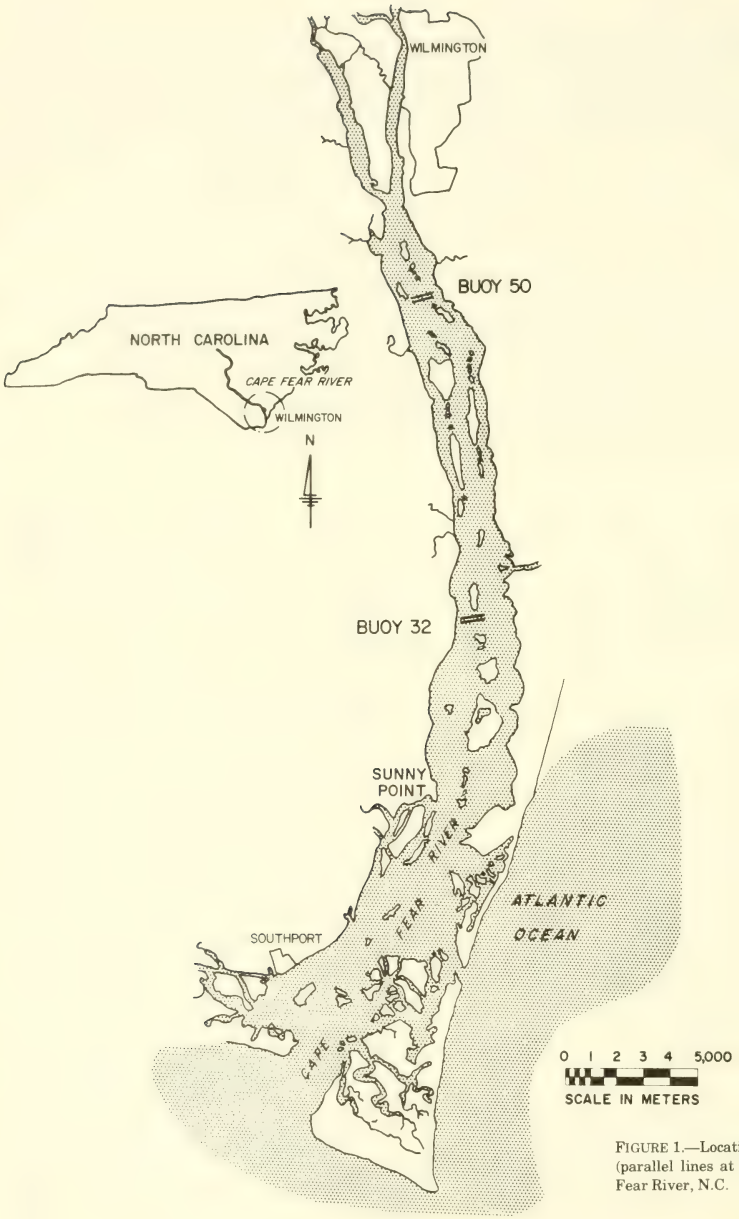


FIGURE 1.—Location of sampling transects (parallel lines at bouys 32 and 50), Cape Fear River, N.C.

formulated which relates these behavioral responses to the maintenance of a preferred position within the estuary.

STUDY AREA

The Cape Fear River estuary (approximately lat. 33° N) is relatively narrow, averaging only 1.6-3.6 km in width and extending 45 km from the general location of the salt boundary at Wilmington, N.C., to the river mouth at Baldhead-Smith Island (Figure 1). A 12 m deep ship channel with a width of 120-150 m is maintained from Wilmington to the river entrance, and adjacent spoil islands are found along its entire length. Tidal velocities in the Cape Fear are high, averaging 2.1 m/s during ebb near the city of Southport, N.C. (National Ocean Survey 1977). Recent hydrographic and dye studies (Carpenter[4]) have established that a two-layer system occurs in the estuary between the vicinity of Sunny Point and Wilmington (Figure 1).

Extensive tidal salt marshes cover about 8,900 ha and form the largest contiguous system of this type in the State of North Carolina (U.S. Army Corps of Engineers[5]). Tidal creeks cover an estimated 648 ha, and shallow open water areas (shoals) between the channel and salt marshes contribute an additional 7,285 ha of suitable nursery habitats for the young of fishes and shellfish.

MATERIALS AND METHODS

A modified version of the gear designed by Graham (1972) was employed in this study (Figure 2A). Individual 0.5 m plankton nets with stainless steel cod end buckets were suspended from aluminum collars (Figure 2B) and bolted onto orienting vanes attached to a 9.5 mm diam-

[4]Carpenter, J. H. 1979. Dye tracer and current meter studies, Cape Fear Estuary 1976, 1977 and 1978. Final report to the Carolina Power & Light Co., Raleigh, N.C., 339 p.

[5]U.S. Army Corps of Engineers. 1977. Maintenance of Wilmington Harbor, North Carolina. Final environmental statement. U.S. Army Engineers District, Wilmington, N.C., 97 p.

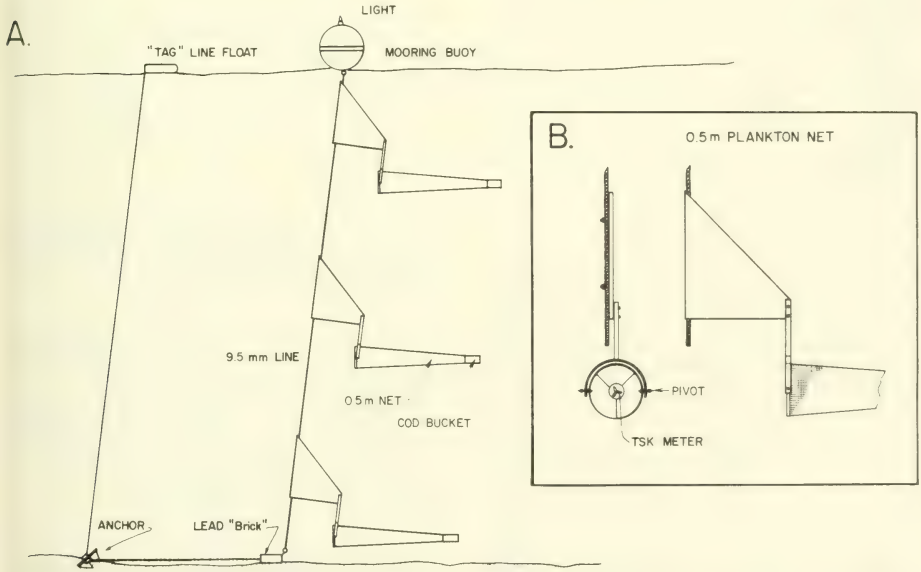


FIGURE 2.—A. Sampling apparatus and deployment, the middepth nets were not used on the east and west shoals. B. Detail of the orienting vane and net mounting. Paired meters were used on all bottom nets.

eter nylon rope. Tidal flows in the Cape Fear estuary were sufficiently high to fully extend these nets during the sampling period. Lead weights (66 kg) between the anchor and bottom net were used to fix the depth at which the bottom nets fished, and a tag line and float attached to the anchor shaft allowed each rig to be easily retrieved at the end of the sampling period. Surface nets were rigged to sample at 1.5 m below the surface, middepth nets at a depth of 6.5 m (in the main channel), and bottom nets, approximately 1 m above the substrate. In order to reduce detection by postlarvae, all nets were dyed deep brown (Rit[6] #20, Cocoa Brown—W. Watson[7]).

Samples were collected at two locations on three sets of dates: 14-15 March, 5-6 April, and 11-12 April. A pair of closely spaced transects were situated near river buoy 50, close to the head of the estuary, and another pair at river buoy 32, at Snow's Cut (Figure 1). Two vessels were employed on each sampling date, and for each transect, three stations were established across the main channel from east to west. At slack water the east and west shoal rigs were set first in 7.6 m of water, and the channel station nets were anchored last. All nets at each of the paired transects were set in <40 min. Because the period of slack water continued for the duration of the setting process, the nets actually began to fish simultaneously and, except for the period of retrieval (about 20 min), a nearly synoptic set of samples was taken across a cross section of the main channel and shoals. On each pair of dates four consecutive tides were sampled, with nets retrieved after 2 h. Limiting the sampling period to 2 h was a necessary precaution in this study because of the potential for net clogging in the highly turbid Cape Fear estuary (see below).

It was planned to sample two nighttime and two daytime tides during each survey but, due to differences in the predicted and actual tides, there was sufficient ambient light to read field data sheets by the end of the last night set at buoy 50 on 6 April. For this reason, the sample was excluded from the analyses.

To reduce the potential for clogging, nets were constructed of 752 μm mesh material and tapered to a length of 3 m. Meshes of this size allowed the passage of many small plankton as well as fine detritus, but retained the postlarvae [$\approx$7-34 mm SL (standard length)] of interest. Previous studies of comparative length frequency in 505 and 760 μm nets (Copeland et al.[8]) indicated that postlarvae <7 mm (of the species of interest) were uncommon in the Cape Fear estuary, since they were recruited from well offshore.

In a preliminary experiment in November 1976, five nets were fished near the bottom, off a tidal creek bridge, and pulled sequentially every 0.5 h after an initial fishing period of approximately 1.0 h (Table 1). The flow past each net was monitored by a TSK[9] meter mounted in the center of the mouth of each net and by a second meter affixed to the collar support. After more than 3 continuous hours of fishing at relatively low flows (compared with the main channel), clogging, as determined by the difference between the inside and outside meter readings, did not exceed 28% on the last net pulled. However, a piece of filamentous algae was found wrapped around the inner TSK prop and axle on this net, restricting free movement. Meter fouling caused by fibrous detritus and algae along the river bottom created considerable difficulties in obtaining useful bottom meter readings in the actual experiments and was deemed a more serious problem than severe net clogging.

In an attempt to overcome bias due to fouled meters, all bottom nets were fitted with paired TSK meters as described above. Based upon the results of the preliminary study (Table 1), it was conservatively estimated that an inside meter

[6]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[7]W. Watson, Associate, Cape Fear Estuarine Laboratory, North Carolina State University, Southport, N.C., pers. commun. September 1976.

[8]Copeland, B. J., R. G. Hodson, and R. J. Monroe. 1979. Larvae and postlarvae in the Cape Fear River estuary, North Carolina, during operation of the Brunswick Steam Electric Plant, 1974-78. Report 79-3 to Carolina Power & Light Co., Raleigh, N.C., 214 p.

[9]Tsurumi Seiki Kosakusho Company.

TABLE 1.—Preliminary net clogging study at Walden Creek, Cape Fear River. Negative percentage difference indicates that inside meter reading was largest.

Net	Time retrieved	Meter	Meter revolutions	Volume (m^3)	% difference (inside/outside)
1	1235	Inside	3,053	97	5
		Outside	3,214		
2	1305	Inside	8,633	275	3
		Outside	8,896		
3	1336	Inside	6,822	217	−7
		Outside	6,357		
4	1406	Inside	14,402	458	9
		Outside	15,812		
5	1437	Inside	12,565	[1]400	28
		Outside	17,410		

[1]A piece of filamentous algae was found wrapped around the TSK prop and axle, restricting free movement.

reading <80% of the outside reading would indicate that the inside meter had fouled. Of the 144 bottom samples collected, 71 had low inside meter readings and 16 had high inside readings. An additional 3 samples were discarded due to gear failure, leaving a total of 54 samples that could be used to obtain an estimator for volume.

A strong linear relationship between inside and outside meter readings ($r = 0.996$, $P<0.01$) indicated that an adequate linear predictor could be obtained:

$$Y = 0.913\,X$$

where Y is the inside meter reading and X is the outside meter reading, both in revolutions. The standard error of the slope of this line is 0.009, and the standard error of an individual estimate of the inner reading is:

$$\mathrm{SE} = \sqrt{7.4729 \times 10^{-5}\,X^2 + 1.758337 \times 10^{6}}\ .$$

The above estimator was used to obtain volumes for all bottom samples in which the inside meter reading was <80% of the outside reading. If a net were actually clogged when we assumed that the meter was fouled, this procedure would result in an overestimate of the volume filtered and underestimate of the actual density of larvae present. Thus, differences among strata would be even larger than depicted in our data.

Upstream and downstream nets at each depth along the paired transects served as replicates in the experiments. This survey constituted a factorial design, with site, photoperiod, and tidal direction as main effects. Nonorthogonal factorial analyses of variance (ANOVA) (Searle 1971) were performed for each taxon, date, and buoy (except spot and Atlantic croaker at buoy 50 on 14-15 March). Examples of the analytical results are reproduced in Appendix I to allow the reader to follow our procedures. A posteriori multiple comparison procedures (Bonferroni t-tests $\alpha = 0.05$; O'Neill and Wetherill 1971) were used to examine station and depth differences and their interactions with photoperiods and tides. Prior to analysis, data were logarithmically transformed [$\log_{10}(10 + X)$] in order to meet the homoscedasticity requirement of ANOVA.

A partial data analysis was performed for 5 April 1978 at buoy 50, deleting the last night set. Either daytime or ebb data alone were used, depending on the strata compared. However, data from all three valid sets were used to obtain an estimate of sampling variability.

All collections were preserved in 5% buffered Formalin, and selected taxa were enumerated and measured for standard length (SL). The latter measurement was taken from the tip of the snout to the end of the notochord or hypural plate. Subsampling for lengths was employed when sorted collections contained >100 individuals of a given species. Data are presented herein on three taxa: spot, *Leiostomus xanthurus*; Atlantic croaker, *Micropogonias undulatus*; and flounders of the genus *Paralichthys*. Flounders were counted but not measured in this program.

RESULTS

Since the April sampling dates were near the end of recruitment for winter-spawned species in the Cape Fear estuary, the observed pattern of distribution during this month should reflect the selection of preferred nursery habitats. On 14-15 March, freshwater flow in the river exceeded 990 m^3/s, and the salt boundary was below buoy 50, as indicated by the absence of measurable salt in the water column. On these dates, spot were entirely absent at buoy 50 and only two Atlantic croaker postlarvae were captured (Figures 3, 4). Flounders, however, were abundant at buoy 50 during this period. When subsequent sampling indicated that the salt front was restored to its normal location, about 6 km above buoy 50, catches of all taxa (with one exception) were significantly greater ($P<0.05$) upstream (Table 2).

Diel Behavior

Significant differences were only occasionally detected among stations and were likely influenced by local patterns of current and larval transport. For this reason, these comparisons were not considered further and were omitted from the ANOVA summary (Table 3). Consistant trends, however, were evident in several other comparisons involving depth, photoperiod, and their interactions. For example, the 24 h mean abundance across depths for spot and Atlantic croaker, and to a lesser degree for flounders, was higher (see also Figures 3, 4) at the bottom on the shoals and at middepth and below in the channel, with essentially no differences between buoys. Photoperiod, on the other hand, influenced the catches of flounder in a consistent manner. Except for 14-15

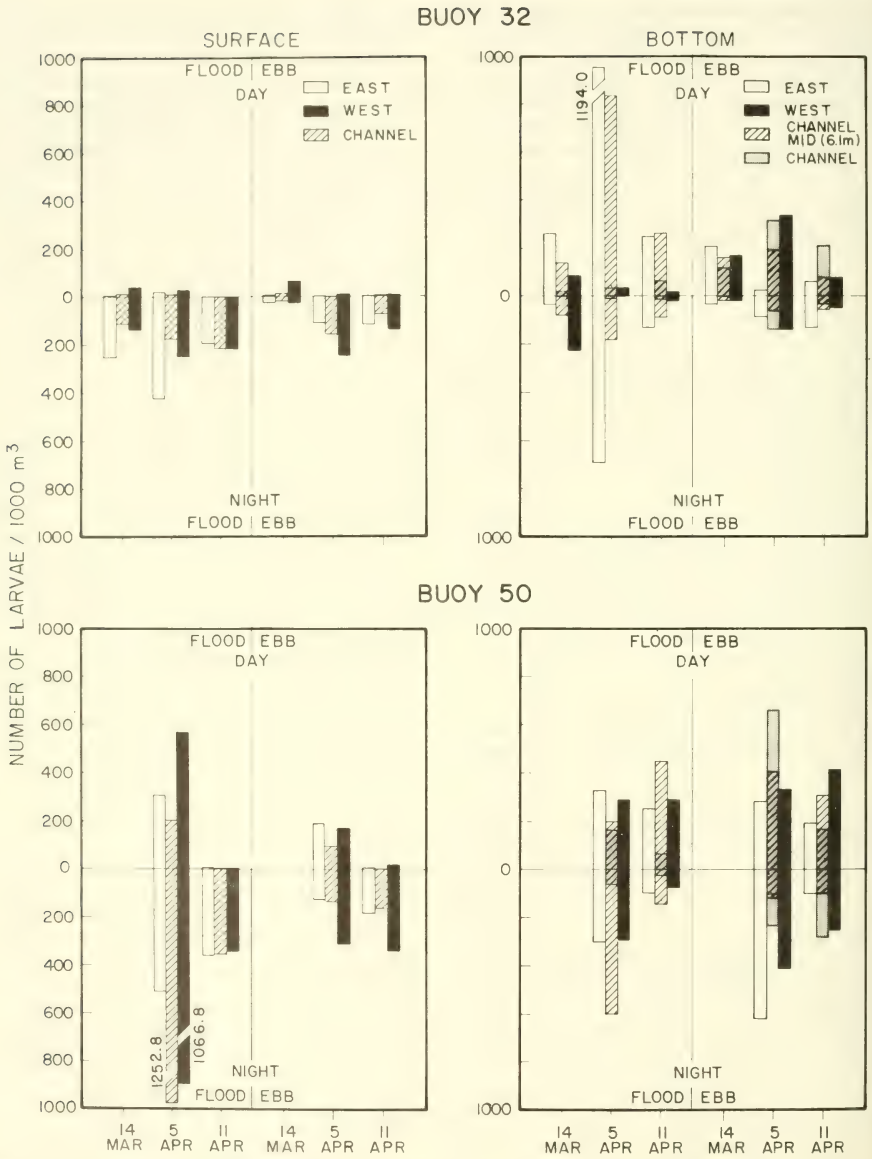


FIGURE 3.—Abundance of spot, *Leiostomus xanthurus*, collected on three sampling dates at buoys 32 and 50. Data are stratified to show mean values for each paired transect with respect to surface-bottom, day-night, and flood-ebb catches. Spot were not captured at buoy 50 on 14-15 March.

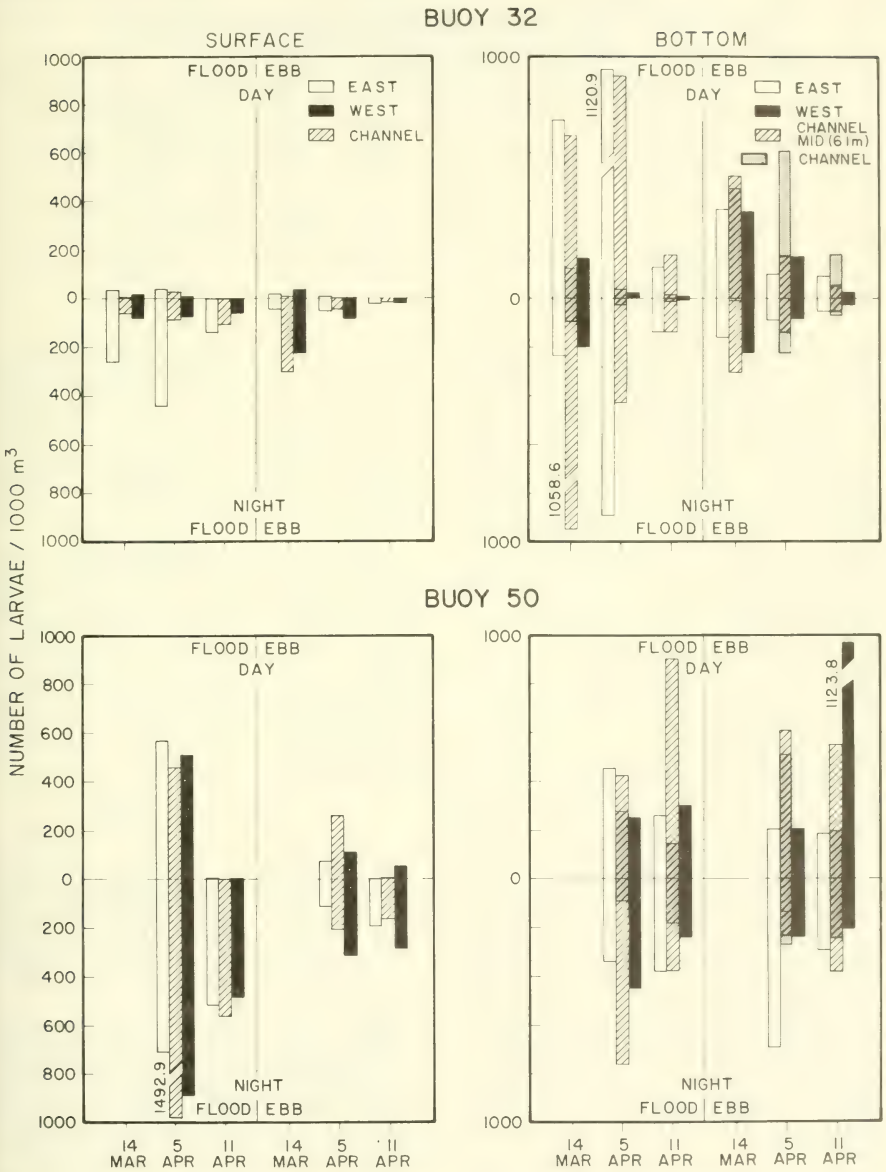


FIGURE 4.—Abundance of Atlantic croaker, *Micropogonias undulatus*, collected on three sampling dates at buoys 32 and 50. Data are stratified to show mean values for each paired transect with respect to surface-bottom, day-night, and flood-ebb catches. Only two croaker were captured at buoy 50 on 14-15 March, these are not shown.

TABLE 2.—Comparison of mean density (number/1,000 m³) at buoy 32 versus buoy 50 for spot, Atlantic croaker, and *Paralichthys* spp.

Date	Spot			Atlantic croaker			*Paralichthys* spp.		
	Buoy	Mean	*t*-value	Buoy	Mean	*t*-value	Buoy	Mean	*t*-value
14-15 Mar.	No analysis conducted						32	46.7	14.76*
							50	147.8	
5-6 Apr.[1]	32	193.4	7.85*	32	189.4	11.55*	32	17.3	1.40
	50	302.7		50	329.3		50	18.0	
11-12 Apr.	32	89.1	8.91*	32	52.6	4.79*	32	2.3	3.64*
	50	179.2		50	294.9		50	3.9	

*Significant at $\alpha = 0.05$; transformed $\log(10 + X)$ data utilizing error mean squares from initial ANOVA's.
[1]Last night set omitted.

March at buoy 50 and 5-6 April at buoy 32, catches at night exceeded those taken during daylight (Table 3). A similar pattern did not emerge for spot and Atlantic croaker, although night values on 11-12 April at both buoys were significantly higher. Apparently, net avoidance was negligible in this study, unlike the findings of Graham (1972), who limited his sampling for larval Atlantic herring to night hours in the Sheepscot estuary because of what he described as excessive daytime net avoidance. High tidal velocities and the turbid waters of the Cape Fear estuary may have been partially responsible for this difference. Flounders were either better able to detect the dyed nets or perhaps exhibited somewhat different diurnal behavior; e.g., a greater tendency to rest on the bottom during the day.

A response to light was further established by an examination of the photoperiod by depth interactions for the three taxa. During the day, spot and Atlantic croaker were most abundant at the bottom and at middepth. Only in the partial data sets analyzed on 5 April 1978 and for Atlantic croaker at buoy 32 on this date was this pattern changed. On this date, depth distributions did not differ for Atlantic croaker and the surface concentration for spot at buoy 50 was not significantly smaller than the channel middepth value. The trend for flounders was similar, although not as distinct as for the other species. At night, all three taxa moved higher in the water column but to differing degrees. Whereas flounders and spot tended to congregate nearer to the surface, most Atlantic croaker remained lower in the water column (Table 3).

Of the five significant photoperiod by depth interactions involving flounders, a posteriori tests conducted for night data indicated that surface concentrations in four instances were significantly greater than at all other depths. Spot also tended to accumulate toward the surface, on the two dates at buoy 32 where a significant interaction was detected, night catches at the surface exceeded those at the bottom; in the main channel, however, surface and middepth concentrations were not significantly different, although the mean for the former always exceeded that of bottom values by a substantial margin.

The best indication of a diel movement by Atlantic croaker occurred in the main channel where the mean for surface night collections diverged less from that of other depths (see also Figure 4), while during the day, the mean for surface collections was usually significantly lower. No surface accumulation was detected for Atlantic croakers on the shoals, on the single date where a significant difference was observed, bottom catches were greater than at the surface.

Response to Tide

Ebb tide catches were generally lower for all taxa than those of corresponding flood tides (Figures 3-5). In addition, a shift in catch density from channel middepth toward the bottom occurred on ebb, and in several instances bottom concentrations exceeded those of middepth nets for all species.

The observed difference between ebb and flood concentrations was always significant for flounders, and on two occasions, for Atlantic croaker. Tide alone did not seem to exert a major influence on the concentrations of spot, although a significant tidal effect was observed on 14-15 March 1978.

All three taxa displayed a trend towards larger flood catches on the eastern shoal and in the channel, while on ebb the western shoal often exhibited

TABLE 3.— Analyses of variance summary, for stations (depths), photoperiod and tides. Station as a main effect is omitted and not all possible interactions are shown. Multiple comparison test results are shown below individual letter designations.

Source		Buoy 32			Buoy 50		
		14 March	5 April	11 April	14 March	5 April[1]	11 April
Depths[2]							
East/west							
Spot		B>S	B>S	B>S	—	(B>S)	B>S
Atlantic croaker		B>S	B>S	B>S	—	(B>S)	B>S
Paralichthys spp.		B>S	ns[3]	ns	ns	(ns)	ns
Channel							
Spot		M B S	M B S	M B S	—	(B M S)	M B S
Atlantic croaker		M B S	M B S	M B S	—	(ns)	M B S
Paralichthys spp.		M S B	ns	ns	ns	(ns)	ns
Photoperiod[4]							
Spot		ns	D>N	N>D	—	(ns)	N>D
Atlantic croaker		ns	D>N	N>D	—	(ns)	N>D
Paralichthys spp.		N>D	D>N	N>D	ns	(N>D)	N>D
Tides[5]							
Spot		F>E	ns	ns	—	(ns)	ns
Atlantic croaker		ns	ns	F>E	—	(F>E)	ns
Paralichthys spp.		F>E	F>E	F>E	F>E	(F>E)	F>E
Photoperiod × depth							
Spot							
East/west	D	B>S	B>S	B>S	—	(ns)	B>S
	N	ns	S>B	S>B	—	(ns)	ns
Channel	D	M B S	M B S	M B S	—	(B M S)	M B S
	N	S M B	S M B	S M B	—	(ns)	S M B
Atlantic croaker							
East/west	D	B>S	B>S	B>S	—	(ns)	B>S
	N	B>S	ns	ns	—	(ns)	ns
Channel	D	M B S	M B S	M B S	—	(ns)	M B S
	N	M B S	ns	M S B	—	(ns)	ns
Paralichthys spp.							
East/west	D	B>S	B>S	ns	ns	(ns)	B>S
	N	ns	S>B	S>B	ns	(ns)	ns
Channel	D	M B S	M B S	M B S	ns	(ns)	ns
	N	M S B	S M B	ns	ns	(ns)	S M B
Tide × station[6]							
Spot							
Flood		E W C	E C W	E C W	—	[ns]	ns
Ebb		ns	W C E	ns	—	[ns]	W C E
Atlantic croaker							
Flood		E C W	E C W	E C W	—	[ns]	ns
Ebb		ns	C W E	C E W	—	[C W E]	W C E
Paralichthys spp.							
Flood		E C W	E C W	ns	ns	[ns]	ns
Ebb		ns	ns	ns	ns	[ns]	W E C
Tide × depth							
Spot							
East/west	F	ns	ns	ns	—	[ns]	ns
	Ebb	B>S	B>S	B>S	—	[ns]	B>S
Channel	F	M S B	M S B	M S B	—	[ns]	M S B
	Ebb	ns	B M S	B M S	—	[B M S]	B M S
Atlantic croaker							
East/west	F	B>S	ns	ns	—	[ns]	B>S
	Ebb	B>S	B>S	B>S	—	[ns]	B>S
Channel	F	M B S	M S B	M S B	—	[ns]	M S B
	Ebb	M B S	B M S	B M S	—	[ns]	M B S
Paralichthys spp.							
East/west	F	ns	ns	ns	ns	[ns]	ns
	Ebb	ns	ns	ns	ns	[ns]	ns
Channel	F	M S B	M S B	ns	ns	[ns]	ns
	Ebb	ns	ns	ns	ns	[ns]	ns

[1][ ]—daytime data only from partial data set on 5 April; ( )—ebb tide data only from partial data set.
[2]Depths: surface (S), middepth (M), bottom (B).
[3]ns—no significant difference at $\alpha = 0.05$ level.
[4]Photoperiods: day (D), night (N).
[5]Tides: flood (F), ebb (E).
[6]Stations: east (E), channel (C), west (W).

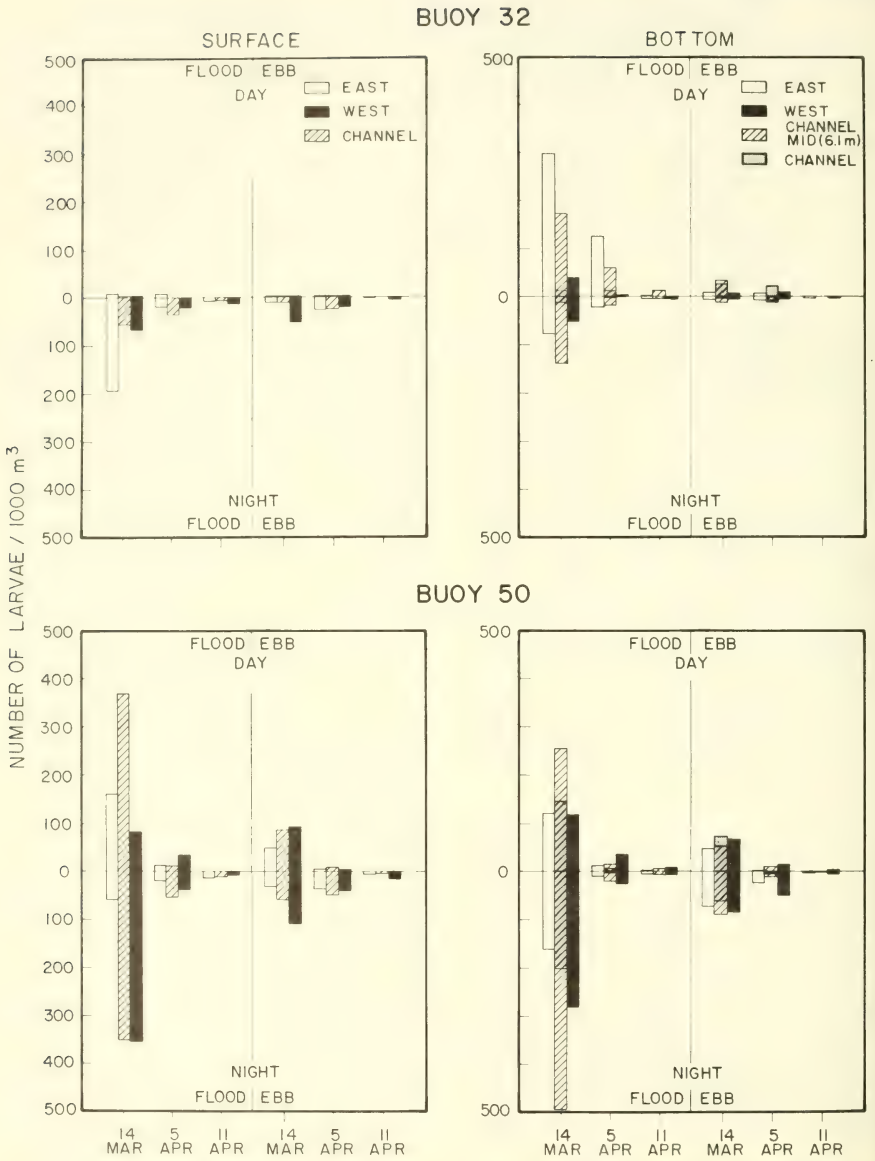


FIGURE 5.—Abundance of flounders (*Paralichthys* spp.) collected on three sampling dates at buoys 32 and 50. Data are stratified to shown mean values for each paired transect with respect to surface-bottom, day-night, and flood-ebb catches.

the largest mean catch. This pattern paralleled the flow of river water between tides; i.e., water tended to move upriver on the eastern shoal and returned on the west. If this phenomenon is real, it indicates the existence of a large-scale circulation pattern for postlarval populations.

The tide by depth interaction clearly described the immediate relationship of these organisms to tidal flows. Whereas the depth distribution of spot on flood tides was fairly uniform, bottom and mid-depth concentrations on ebb often exceeded those of surface values. Results were not quite as clear for Atlantic croaker because of their general bottom orientation; nevertheless, a tidal response was still evident for this species (Figure 4). Paradoxically, flounder showed little response to tide (compared with the main effect result), although a pattern similar to that of the other species is shown in the mean concentrations in Figure 5.

All of these comparisons are potentially influenced by diel activity, i.e., by downward migration during the day. Mean bottom values are influenced by this effect on both flood and ebb during daylight hours. One way of isolating the effect of photoperiod would be to examine the interaction of the three main effects (Table 3). Unfortunately, this interaction was rarely significant. Lack of significance may be a consequence of the use of a logarithmic scale in making comparisons. Also, the power of tests on this three-way interaction is considerably less than that of tests of main effects and of two-way interactions. That diel migration was not entirely responsible for the observed patterns may be seen in the overall (24 h) differences between flood and ebb. Since two flood and ebb tides were sampled over each 24-h period, the effect of diel activity should be manifested on both tides; i.e., bottom orientation should occur on flood as well. Table 3 indicates that this was not the case. Furthermore, a perusal of the individual strata in Figures 3-5; e.g., an examination of surface night concentrations alone, shows that a clear tidal response was exhibited by all three species.

Length-Frequency Distributions

The possibility that buoy 50 was located within a primary nursery zone was alluded to earlier. This contention is also supported by length-frequency data which show that larger (older) fish tended to accumulate upriver near buoy 50. Unfortunately, larger fishes were probably not captured quantitatively since gear efficiency drops off rapidly after about 30 mm SL (Copeland et al. see footnote 8). Hence, only a qualitative picture of the age composition of a year class is possible. Nevertheless, distinct size differences occurred between buoys as indicated in Figures 6 and 7.

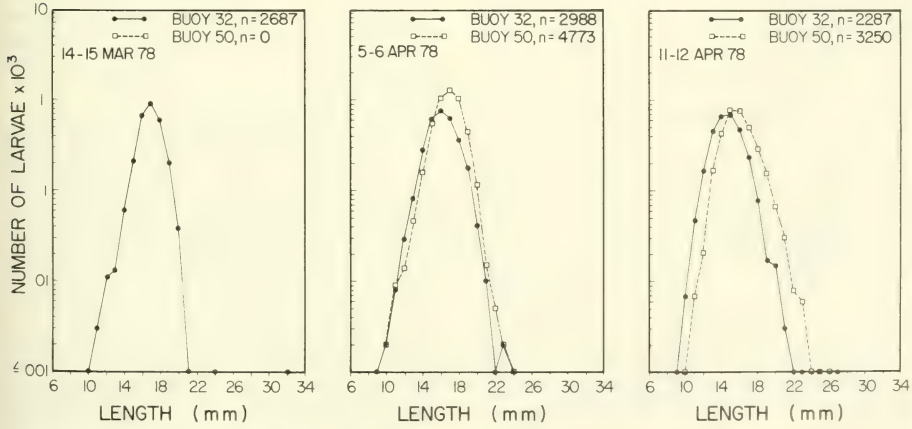


FIGURE 6.—Length-frequency distribution for spot, *Leiostomus xanthurus*, on the three collecting dates. This species was entirely absent from the vicinity of buoy 50 on 14-15 March.

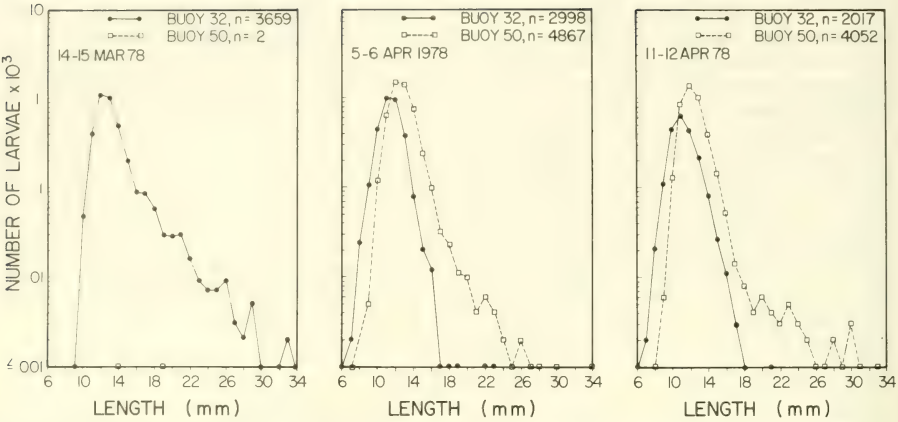


FIGURE 7.—Length-frequency distribution for Atlantic croaker, *Micropogonias undulatus*, on the three collecting dates. Only two individuals were captured in the vicinity of buoy 50 on 14-15 March.

Most interestingly, during the high-flow period on 14-15 March 1978, when spot and Atlantic croaker moved downriver, the larger fish accompanied the newer recruits to the vicinity of buoy 32. This is most evident in Figure 7 for Atlantic croaker. With the return of the salt front above buoy 50 in April, spot and Atlantic croaker returned upstream. For both species in this month, length-frequency distributions at buoys 32 and 50 were compared by Pearson chi-square tests. Significant differences ($P<0.05$) were found for all comparisons, with larger fish predominating upstream.

DISCUSSION

In contemplating the retention of bivalve larvae within the James River estuary, Wood and Hargis (1971) stated, "The point at issue is not whether such retention occurs, but whether evolved patterns of larval behaviour contribute significantly to the process." Evidence from the present investigation supports the premise that, by displaying specific behavioral responses, postlarvae of the three taxa studied were able to reach and stay within specific portions of the Cape Fear River estuary. This occurred despite intensive tidal flows and relatively high exchange ratios in the system.

Peak recruitment for winter-spawned larvae in the Cape Fear estuary and many other Atlantic coast estuaries occurs at a time when stratification and tidal exchange ratios are usually at a yearly maximum. The exchange ratio may exceed 0.70 in the Cape Fear estuary and flows above 1,700 m^3/s have been recorded in January and February 1978 (Carpenter see footnote 4). Species recruited from the ocean also have the peculiar problem of initial entrance into the estuary and the avoidance of being washed out on the subsequent tide. By responding to a combination of hydrographic features of the estuary and perhaps to exogenous variables these species are able to avoid net seaward transport.

Active responses to light and diel migrations in the water column have been attributed to the larvae of barnacles (Fales 1928; Bassindale 1936; Bousfield 1955), oysters and other bivalves (Carriker 1951; Korringa 1952; Williams and Porter 1971: Wood and Hargis 1971), copepods (Schallek 1943), shrimp (Hughes 1969a, b, 1972; Williams and Deubler 1968), and fishes (Rogers 1940; Creutzberg 1961; Pacheco and Grant 1968; Lewis and Wilkens 1971; Graham 1972; Smith et al. 1978). However, differential avoidance of nets with respect to depth has also sometimes been suggested as the cause of diel "migrations" (e.g., Fore and Baxter 1972). Results of comparative studies using several kinds of collecting gear, including high-speed trawls (Thayer et al. in press), and the observed absence or low abundance of

most species (including those studied here) in daylight entrainment collections at a power plant located on the river near Southport (Copeland et al. see footnote 8) imply that this hypothesis is not tenable and support the contention that diel migrations actually do take place. If larvae were similarly stratified in the water column with respect to tide, a result paralleling that of the photoperiod response would be expected. By resting on the substratum during ebb, or at least by moving downward in the water column (below the level of no net motion), larvae would be transported in the landward direction.

Behavioral responses of spot, Atlantic croaker, and flounders to photoperiod and tide are summarized in Figure 8. Several important differences delineate ultimate habitat utilization by these species. Flounders apparently reacted to tidal flows by settling to the bottom, as has been suggested for oysters and shrimps (Carriker 1951; Hughes 1969a, b, 1972). When the lack of significant tide by depth interaction and the presence of a tidal main effect are considered together, this hypothesis seems more tenable. To a degree, seeking boundary layers may be a general tidal response exhibited by all three species, making them difficult to sample on ebb (especially since the bottom nets were set 1 m above the substrate). The ability of flounders to effectively penetrate freshwaters also is enhanced by this behavior. Tidal flows above the salt boundary are substantial, certainly greater than the ability of flounder postlarvae to negotiate them directly. Saltatory movement upriver by "riding out" ebb on the bottom and responding to currents on flood would then be a primary mechanism for continued upstream migration.

Both spot and flounders were also observed to migrate toward the surface at night; significantly larger numbers of individuals were captured in this stratum both in midchannel and on the shoals, while Atlantic croaker tended to remain

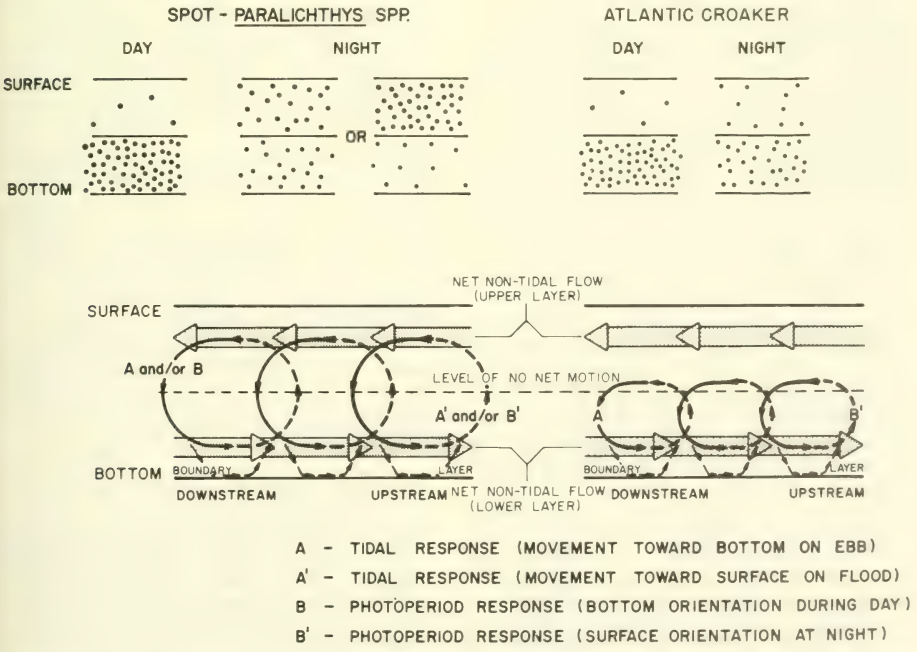


FIGURE 8.—Conceptual model for a larval retention mechanism based on response to photoperiod and tide. Details of the response differ for the three taxa (see text).

bottom oriented during this period. In studies of feeding by postlarval fishes in the Newport River estuary, N.C., Peters and Kjelson (1975) and Kjelson et al. (1975) demonstrated that spot were actively feeding only during the daytime and described them as carnivorous sight feeders. If the nighttime surface orientation observed for flounders and spot is not related to feeding activity, then to what might it be attributed?

We suggest that active migration into the marshes is aided by surface movement on flood tide at night. Since the mouths of many of these tidal creeks have sills, and since most are shallow and lack stratification, remaining near the bottom in the main stem would not aid postlarvae in lateral movements into the marshes. However, by staying near the surface on night flood tides, large numbers of individuals would be carried laterally into the marshes and other shoal areas, perhaps with the additional advantage of lower predation pressure.

Once in the marsh or other suitable shallow area, a tidal response elicited on ebb, i.e., a tendency to seek boundary layers near the bottom or toward the banks, would allow at least some members of the cohort carried into the system on flood to remain on ebb (Lewis and Mann 1971). This percentage need not be very high on each tidal cycle to produce a rapid population accumulation.

Species displaying a greater tendency to remain in the lower layers over 24 h should not be present in great numbers in shallow areas. This is precisely the case for Atlantic croaker. The marshes in the Cape Fear are not a major nursery zone for this species, as demonstrated by the nearly complete absence of postlarval Atlantic croaker from this habitat (Weinstein 1979). A noteworthy paradox arises when this species is considered over most of its geographic range. Atlantic croaker seem to prefer those estuaries with deep channels and are not taken in large numbers in the shallows (Welsh and Breder 1923; Wallace 1941; Suttkus 1955; Haven 1957; Nelson 1969; Chao and Musick 1977). It is suspected that in these estuaries, postlarval Atlantic croaker maintain their general bottom orientation and do not move laterally to any great extent; however, in several shallow estuaries along the Gulf of Mexico (Herke 1971; Parker 1971; Arnoldi et al. 1974; Yakupzack et al. 1977) young Atlantic croaker make extensive use of the marsh shallows. Thus, in those situations where deep channels are not predominant features of the system, Atlantic croaker will make use of the marsh shallows. This difference in distribution in the Gulf States might be further reconciled if temperature is taken into consideration. Temperature as a potential limiting factor for Atlantic croaker year class success in most middle Atlantic coast estuaries has been discussed by Joseph (1972). Remaining in the warmer waters of the deep channel during winter might enhance Atlantic croaker survival. The winters of 1976-77 and 1977-78 along the Atlantic coast have been colder than usual; greater utilization of shallow areas by Atlantic croaker might occur in warmer years.

Others also have observed that the river main stem at the head of the Cape Fear estuary is a primary nursery zone for Atlantic croaker and, to a more limited extent, for spot and flounders (Copeland et al. see footnote 8). In addition, the boundaries of this zone for certain species are dictated by freshwater flows and tend to shift with these flows. Although not captured quantitatively, larger spot and Atlantic croaker accumulated upriver in the vicinity of buoy 50 (Figures 6, 7). Although flounders were not measured, a similar result would be expected for these species.

In summary, we believe the data presented are consistent with the hypothesis that postlarvae exhibit behavioral patterns with respect to photoperiod and tide which are instrumental in enabling these organisms to: 1) accumulate in upstream nurseries by utilizing net nontidal flows in the lower layer, 2) make strong lateral movements into the marsh nurseries by migrating to the surface on flood tide at night, and 3) stay in both of these primary nurseries by dropping lower into or effectively out of the water column on ebb. The tidal response may be particularly important in well-mixed estuaries where upstream drift in the lower layers is negligible. In fact, it might be the primary mechanism employed by postlarvae to penetrate estuaries and reach suitable nursery habitats.

ACKNOWLEDGMENTS

We are grateful to the biotechnicians of Lawler, Matusky & Skelly Engineers (LMS) for their conscientious efforts in the field and laboratory and to W. Werth for his assistance in constructing the sampling gear. We also would like to thank K. L. Heck, Jr., D. T. Logan, J. P. Lawler, and R. L. Wyman for their many useful suggestions for improving the manuscript. Appreciation is extended

to S. Moy (statistician) and M. Walters for their efforts in completing data analyses, and to the editorial staff of LMS, especially B. Marlowe, B. Schwartzberg, and M. Barker, for their aid in editing and typing the manuscript. This study was funded by the Carolina Power and Light Company.

LITERATURE CITED

ARNOLDI, D. C., W. H. HERKE, AND E. J. CLAIRAIN, JR.
1974. Estimate of growth rate and length of stay in a marsh nursery of juvenile Atlantic croaker, *Micropogon undulatus* (Linnaeus), "sandblasted" with fluorescent pigments. Gulf Caribb. Fish. Inst., Proc. 26th Annu. Sess., p. 158-172.

BASSINDALE, R.
1936. The developmental stages of three English barnacles *Balanus balanoides* (Linn.), *Chthamalus stellatus* (Poli), and *Verruca stroemia* (Muller). Proc. Zool. Soc. Lond. 1936, Part I:57-74.

BOUSFIELD, E. L.
1955. Ecological control of the occurrence of barnacles in the Miramichi estuary. Natl. Mus. Can., Bull. 137, 69 p.

CARRIKER, M. R.
1951. Ecological observations on the distribution of oyster larvae in New Jersey estuaries. Ecol. Monogr. 21:19-38.

CHAO, L. N., AND J. A. MUSICK.
1977. Life history, feeding habits, and functional morphology of juvenile sciaenid fishes in the York River estuary, Virginia. Fish. Bull., U.S. 75:657-702.

CREUTZBERG, F.
1961. On the orientation of migrating elvers (*Anguilla vulgaris* Turt.) in a tidal area. Neth. J. Sea Res. 1:257-338.

FALES, D. E.
1928. The light-receptive organs of certain barnacles. Biol. Bull. (Woods Hole) 54:534-547.

FORE, P. L., AND K. N. BAXTER.
1972. Diel fluctuations in the catch of larval Gulf menhaden, *Brevoortia patronus*, at Galveston Entrance, Texas. Trans. Am. Fish. Soc. 101:729-732.

GRAHAM, J. J.
1972. Retention of larval herring within the Sheepscot estuary of Maine. Fish. Bull., U.S. 70:299-305.

HAVEN, D. S.
1957. Distribution, growth and availability of juvenile croaker, *Micropogon undulatus*, in Virginia. Ecology 38:88-97.

HERKE, W. H.
1971. Use of natural, and semi-impounded, Louisiana tidal marshes as nurseries for fishes and crustaceans. Ph.D. Thesis, Louisiana State Univ., Baton Rouge, 264 p.

HUGHES, D. A.
1969a. Responses to salinity change as a tidal transport mechanism of pink shrimp, *Penaeus duorarum*. Biol. Bull. (Woods Hole) 136:43-53.
1969b. On the mechanisms underlying tide-associated movements of *Penaeus duorarum* Burkenroad. FAO Fish. Rep. 57:867-874.
1972. On the endogeneous control of tide-associated displacements of pink shrimp, *Penaeus duorarum* Burkenroad. Biol. Bull. (Woods Hole) 142:271-280.

JOSEPH, E. B.
1972. The status of the Sciaenid stocks of the middle Atlantic coast. Chesapeake Sci. 13:87-100.

KJELSON, M. A., D. S. PETERS, G. W. THAYER, AND G. N. JOHNSON.
1972. The general feeding ecology of postlarval fishes in the Newport River estuary. Fish. Bull., U.S. 73:137-144.

KORRINGA, P.
1952. Recent advances on oyster biology. Q. Rev. Biol. 27:266-365.

LEWIS, R. M., AND W. C. MANN.
1971. Occurrence and abundance of larval Atlantic menhaden, *Brevoortia tyrannus*, at two North Carolina inlets with notes on associated species. Trans. Am. Fish. Soc. 100:296-301.

LEWIS, R. M., AND E. P. H. WILKENS.
1971. Abundance of Atlantic menhaden larvae and associated species during a diel collection at Beaufort, North Carolina. Chesapeake Sci. 12:185-187.

NATIONAL OCEAN SURVEY.
1977. Tidal current tables 1978: Atlantic coast of North America. U.S. Dep. Commer., 214 p.

NELSON, W. R.
1969. Studies on the croaker, *Micropogon undulatus* Linnaeus, and the spot, *Leiostomus xanthurus* Lacepede, in Mobile Bay, Alabama. J. Mar. Sci. Ala. 1:4-92.

O'NEILL, R., AND G. B. WETHERILL.
1971. The present state of multiple comparison methods. J. R. Stat. Soc., Ser. B, 33:218-241.

PACHECO, A. L., AND G. C. GRANT.
1968. Immature fishes associated with larval Atlantic menhaden at Indian River inlet Delaware, 1958-61. *In* A. L. Pacheco (editor), Proceedings of a workshop on egg, larval, and juvenile stages of fish in Atlantic Coast estuaries, p. 70-117. U.S. Dep. Commer., Natl. Mar. Fish. Serv. Tech. Publ. 1.

PARKER, J. C.
1971. The biology of the spot, *Leiostomus xanthurus* Lacepède, and the Atlantic croaker, *Micropogon undulatus* (Linnaeus), in two Gulf of Mexico nursery areas. Ph.D. Thesis, Texas A&M Univ., College Station, 236 p.

PEARCY, W. G., AND S. W. RICHARDS.
1962. Distribution and ecology of fishes of the Mystic River estuary, Connecticut. Ecology 43:248-259.

PETERS, D. S., AND M. A. KJELSON.
1975. Consumption and utilization of food by various postlarval and juvenile fishes of North Carolina estuaries. *In* E. L. Cronin (editor), Estuarine research, Vol. 1, Chemistry, biology and the estuarine system, p. 448-472. Acad. Press, N.Y.

ROGERS, H. M.
1940. Occurrence and retention of plankton within the estuary. J. Fish. Res. Board Can. 5:164-171.

SANDIFER, P. A.
1975. The role of pelagic larvae in recruitment to populations of adult decapod crustaceans in the York River estuary and adjacent lower Chesapeake Bay, Virginia. Estuarine Coastal Mar. Sci. 3:269-279.

SCHALLEK, W.
1943. The reaction of certain crustacea to direct and diffuse light. Biol. Bull. (Woods Hole) 84:98-105.

SEARLE, S. R.
1971. Linear models. Wiley, N.Y., 532 p.

SMITH, W. G., J. D. SIBUNKA, AND A. WELLS.
1978. Diel movements of larval yellowtail flounder, *Limanda ferruginea*, determined from discrete depth sampling. Fish. Bull., U.S. 76:167-178.

SUTTKUS, R. D.
1955. Seasonal movements and growth of the Atlantic croaker (*Micropogon undulatus*) along the east Louisiana coast. Proc. Gulf Caribb. Fish. Inst., 7th Annu. Sess., p. 151-158.

THAYER, G. W., D. R. COLBY, M. A. KJELSON, M. P. WEINSTEIN, M. W. LACROIX, G. B. MONTGOMERY, AND G. N. JOHNSON.
In press. Influence of tow speed on abundance estimates for larval fishes near Beaufort, North Carolina. J. Fish. Res. Board Can.

TURGEON, D. D.
1976. Distribution of the planktonic larvae of some benthic invertebrates within the Piscataqua-Great Bay Estuary, New Hampshire. Ph.D. Thesis, Univ. New Hampshire, Durham, 165 p.

WALLACE, D. H.
1941. Sexual development of the croaker, *Micropogon undulatus*, and distribution of the early stages in Chesapeake Bay. Trans. Am. Fish. Soc. 70:475-482.

WEINSTEIN, M. P.
1979. Shallow marsh habitats as primary nurseries for fishes and shellfish, Cape Fear River, North Carolina. Fish. Bull., U.S. 77:339-357.

WELSH, W. W., AND C. M. BREDER, JR.
1923. Contributions to life histories of the Sciaenidae of the eastern United States coast. Bull. [U.S.] Bur. Fish. 39:141-201.

WILLIAMS, A. B., AND E. E. DEUBLER.
1968. A ten-year study of meroplankton in North Carolina estuaries: Assessment of environmental factors and sampling success among bothid flounders and penaeid shrimps. Chesapeake Sci. 9:27-41.

WILLIAMS, A. B., AND H. J. PORTER.
1971. A ten-year study of meroplankton in North Carolina estuaries: occurrence of postmetamorphal bivalves. Chesapeake Sci. 12:26-32.

WOOD, L., AND W. J. HARGIS, JR.
1971. Transport of bivalve larvae in a tidal estuary. 4th Eur. Mar. Biol. Symp., p. 29-44.

YAKUPZACK, P. M., W. H. HERKE, AND W. G. PERRY.
1977. Emigration of juvenile Atlantic croakers, *Micropogon undulatus*, from a semi-impounded marsh in southwestern Louisiana. Trans. Am. Fish. Soc. 106:538-544.

APPENDIX TABLE 1.—Three-way analysis of variance for spot, *Leiostomus xanthurus*, postlarvae captured at buoy 32, 14-15 March 1978. Catch data are $\log_{10}(10 + X)$ transformed.

Source	df	SS	MS	*F*	Source	df	SS	MS	*F*
Photoperiod, P	1	0.0551	0.0551	1.50	P × S	6	3.2729	0.5455	14.83*
Tide, T	1	0.2218	0.2218	6.03*	T × S	6	0.5744	0.9057	2.60*
Sites, S	6	2.6871	0.4479	12.17*	P × T × S	6	0.3805	0.0634	1.72
P × T	1	1.2493	1.2493	33.95*	Error	24	0.8831	0.0368	

Multiple comparisons (Numbers in parentheses are mean catch for each stratum.)

A. Tides
Flood (100.7) > ebb (68.2)

B. Sites (Bonferroni *t*-tests; $\alpha = 0.05$)
1. Depths: east and west
Bottom (131.9) > surface (68.3)
2. Depths: channel
Largest: middepth(97.1) bottom (39.3) surface(39.2): smallest
3. Stations
Largest: east(109.5) west(90.6) channel(58.5): smallest

C. Photoperiod × tide (Bonferroni *t*-tests; $\alpha = 0.05$)
Largest: flood/night(120.3) ebb/day(103.3) flood/day(81.1) ebb/night (27.2): smallest

D. Photoperiod × site (bonferroni *t*-tests; $\alpha = 0.05$)
1. Photoperiod × depth: east and west
Day: bottom(178.5) > surface(25.0)
Night: ns[†]
2. Photoperiod × depth: channel
Day; largest: middepth(145.0) bottom(65.9) surface(8.8): smallest
Night; largest: surface(79.5) middepth(49.2) bottom(3.9): smallest
3. Photoperiod × station
Day: ns
Night; largest: west(97.8) east(91.1) channel(44.3): smallest

E. Tide × site (Bonferroni *t*-tests; $\alpha = 0.05$)
1. Tide × depth: east and west
Flood: ns
Ebb: bottom(112.6) > surface(31.3)
2. Tide × depth: channel
Flood; largest: middepth(108.5) surface(58.1) bottom(9.3): smallest
Ebb: ns
3. Tide × station
Flood; largest: east(158.6) west(110.1) channel(58.6): smallest
Ebb: ns

*Significant at $\alpha = 0.05$.
[†]ns—no significant difference(s).

APPENDIX TABLE 2.—Three-way analysis of variance for Atlantic croaker, *Micropogonias undulatus*, postlarvae captured at buoy 32, 14-15 March 1978. Catch data are $\log_{10}(10 + X)$ transformed.

Source	df	SS	MS	F	Source	df	SS	MS	F
Photoperiod, P	1	0.0594	0.0594	1.46	P × S	6	2.1754	0.3626	8.91*
Tide, T	1	0.1086	0.1086	2.67	T × S	6	0.6195	0.1033	2.54*
Sites, S	6	9.3385	1.5564	38.24*	P × T × S	6	0.5752	0.0959	2.36
P × T	1	0.5152	0.5152	12.66*	Error	24	0.9769	0.0407	

Multiple comparisons (Numbers in parentheses are mean catch for each stratum.)

A. Photoperiod × tide (Bonferroni t-tests; $\alpha = 0.05$)
   Largest: flood/night(301.4) ebb/day(249.7) flood/day(266.6) ebb/night(143.5): smallest

B. Sites (Bonferroni t-tests; $\alpha = 0.05$)
   1. Depths: east and west
      Bottom (311.6)>surface (69.5)
   2. Depths: channel
      Largest: middepth(636.6) bottom(193.2) surface(28.1): smallest
   3. Stations: ns[1]

C. Photoperiod × site (Bonferroni t-tests; $\alpha = 0.05$)
   1. Photoperiod × depth: east and west
      Day: bottom(404.6)>surface(25.7)
      Night: bottom(218.5)>surface(107.0)
   2. Photoperiod × depth: channel
      Day; largest: middepth(590.9) bottom(288.7) surface(6.3): smallest
      Night; largest: middepth(682.2) bottom(65.9) surface(57.2): smallest
   3. Photoperiod × station
      Day: ns
      Night: ns

D. Tide × site (Bonferroni t-tests; $\alpha = 0.05$)
   1. Tide × depth: east and west
      Flood: bottom(336.3)>surface(110.7)
      Ebb: bottom(286.8)>surface(38.7)
   2. Tide × depth: channel
      Flood; largest: middepth(865.7) bottom(110.0) surface(31.6): smallest
      Ebb; largest: middepth(407.4) bottom(304.2) surface(23.6): smallest
   3. Tide × station
      Flood; largest: east(336.8) channel(335.8) west(110.1)
      Ebb: ns

*Significant at $\alpha = 0.05$.
[1]ns—no significant difference(s).

APPENDIX TABLE 3.—Three-way analysis of variance for *Paralichthys* spp. postlarvae captured at buoy 32, 14-15 March 1978. Catch data are $\log_{10}(10 + X)$ transformed.

Source	df	SS	MS	*F*	Source	df	SS	MS	*F*
Photoperiod, P	1	0.3217	0.3217	12.55*	P × S	6	1.7818	0.2970	11.58*
Tide, T	1	2.5208	2.5208	98.32*	T × S	6	1.1400	0.1900	7.41*
Sites, S	6	1.8388	0.3065	11.95*	P × T × S	6	0.4869	0.0812	3.17*
P × T	1	0.2309	0.2309	9.00*	Error	24	0.6154	0.0256	

Multiple comparisons (Numbers in parentheses are mean catch for each stratum.)

A. Photoperiod
Night (50.3)>day (45.7)

B. Tide
Flood(84.7)>ebb(11.1)

C. Sites (Bonferroni *t*-tests; $\alpha = 0.05$)
1. Depths: east and west; bottom (62.3)>surface (37.8)
2. Depths: channel
Largest: middepth(89.8) surface(20.3) bottom(14.9): smallest
3. Stations largest: east(79.3) channel(41.6) west(20.8): smallest

D. Photoperiod × tide (Bonferroni *t*-tests; $\alpha = 0.05$)
Largest: flood/night(87.0) flood/day(82.3) ebb/night (10.5) ebb/day(11.6): smallest

E. Photoperiod × site (Bonferroni *t*-tests; $\alpha = 0.05$)
1. Photoperiod × depth: east and west
Day: bottom(89.0) >surface(3.4)
Night: ns[1]
2. Photoperiod × depth: channel
Day; largest: middepth(103.4) bottom(19.1) surface(1.9): smallest
Night; largest: middepth(76.1) surface(44.8) bottom(9.2): smallest
3. Photoperiod × station
Day: ns
Night; ns

F. Tide × site (Bonferroni *t*-tests; $\alpha = 0.05$)
1. Tide × depth: east and west
Flood: ns
Ebb: ns
2. Tide × depth: channel
Flood; largest: middepth(156.4) surface(29.4) bottom(12.4): smallest
Ebb: ns
3. Tide × station
Flood; largest: east(160.3) channel(66.1) west(35.5): smallest
Ebb: ns

*Significant at $\alpha = 0.05$.
[1]ns—no significant difference(s).

RELATIONSHIPS BETWEEN WAVE DISTURBANCE AND ZONATION OF BENTHIC INVERTEBRATE COMMUNITIES ALONG A SUBTIDAL HIGH-ENERGY BEACH IN MONTEREY BAY, CALIFORNIA

JOHN S. OLIVER, PETER N. SLATTERY, LARRY W. HULBERG, AND JAMES W. NYBAKKEN[1]

ABSTRACT

Benthic marine invertebrate communities were organized along a gradient of wave-induced substrate motion on the subtidal high-energy beach in Monterey Bay, California. Two general zones were distinguished from 6 to 30 m of water. A shallow zone (<14 m) contained sediments that were commonly disrupted by wave activity and it was primarily occupied by small, mobile, deposit-feeding peracarid and ostracod crustaceans. Patterns of crustacean morphology and mobility were related to their depth zonation. Few animals lived in permanent tubes or burrows in the crustacean zone. Wave disturbance decreased with increasing water depth, while the numbers of sessile and semisessile species, commensal animals, and suspension or selective-surface-deposit feeders increased. The deeper zone (>14 m) was dominated by polychaete worms living in relatively permanent tubes and burrows. A variety of descriptive-correlative evidence indicates that community zonation is strongly influenced by wave-induced bottom disturbance. The evidence includes: 1) a positive correlation between water depth and the numbers of tube dwellers, burrow dwellers, and commensal animals which apparently cannot establish or maintain populations in shifting sediments; 2) other depth and thus substrate disturbance related natural history patterns; 3) a positive correlation between the strength of wave activity and the width and depth limits of the faunal zones (i.e., when wave disturbance is more intense, the crustacean zone ends and the polychaete zone begins in deeper water); 4) a correspondence between the largest decrease in polychaete population size and the season and location of greatest wave activity (winter months at the shallowest station); and 5) a marked similarity between community zonation along a depth-dependent gradient of oscillatory substrate motion (gently sloping sandflats) and the zonation along a constant depth gradient of creeping substrate motion (submarine canyon ridge). Other explanations are inconsistent with these biological patterns and, thus, wave disturbance is apparently the major physical process affecting community zonation.

Sedimentary environments are dynamic and strongly influenced by water currents and the physical and biological properties of the sediment. These animal-sediment relations have become a major focus of benthic community studies since the pioneering work of Sanders (1958, 1960) and Rhoads and Young (1970) and were recently reviewed by Rhoads (1974) and Gray (1974). This previous work was primarily restricted to wave-protected embayments where deposition and resuspension of fine sediments is a major process. In contrast, the open-coastal environment is commonly subjected to oceanic swell which has a dramatic effect on substrate motion (e.g., Komar 1976). Although sediment scour and motion are major sedimentary processes affecting the shallow parts of most continental shelves, little is known about their effect on the establishment and maintenance of soft-bottom communities.

The large areal scale of gradients in wave-induced bottom disturbance and the corresponding community patterns are difficult to manipulate experimentally. However, potential relationships between wave disturbance and community zonation can be explored by a posteriori correlations and by a priori use of "natural experiments" (sensu Cody 1974). While communities are often organized along gradients of environmental variability (Whittaker 1962, 1967; Mills 1969; Nichols 1970), the complex interactions between physical and biological regulatory processes are rarely understood. The descriptive and experimental studies in the marine rocky intertidal habitat are an important exception (e.g., Connell 1961; Dayton 1971; Ricketts et al. 1972; Stephenson and Stephenson 1972; Paine 1974; Lubchenco and Menge 1978). This study has two primary objectives: to describe the zonation of benthic inverte-

[1]Moss Landing Marine Laboratories, P.O. Box 223, Moss Landing, CA 95039.

Manuscript accepted November 1979.
FISHERY BULLETIN: VOL. 78, NO. 2, 1980.

brates along a subtidal high-energy beach; and to examine the relationship between community zonation and wave-induced bottom disturbance. Understanding the role of this predominant physical process is critical to subsequent studies of biological phenomena and their interactions with the physical sedimentary environment.

METHODS

The study area was in central Monterey Bay, Calif., on the sandflats adjacent to the Monterey Submarine Canyon and along a ridge in the canyon head (Figure 1). The southern sandflat transect was the main study site (Figures 1, 2). Stations in 6 (M-1), 9 (M-2), 14 (M-3), 18 (M-4), and 24 m (M-5) of water were sampled at approximately the same time from June 1971 to June 1974. Three stations (9, 18, 24 m) were sampled along the northern sandflat from August 1974 to June 1975 (Figure 1; N stations). The maximum interval between sampling periods was 3 mo. Therefore, samples were taken during at least the four major seasons at each station. The two deepest stations along the northern sandflat (N-5, 30 m; N-6, 40 m) were only sampled in May 1975. Samples were treated separately to document seasonal patterns and were combined over the study period for each station to examine general zonal patterns.

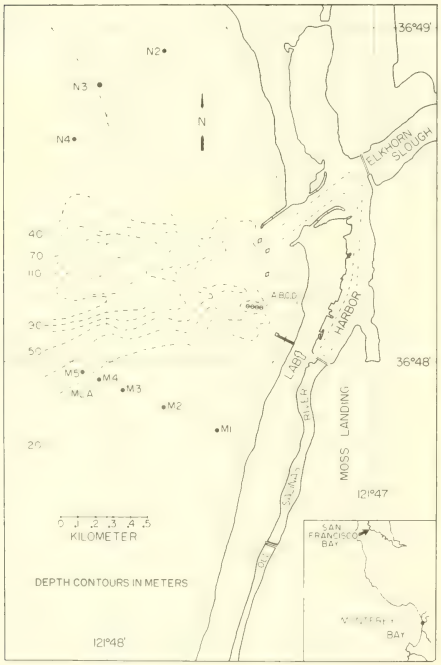


FIGURE 1.—Southern (M) and northern (N) sandflat stations and the canyon transect (A-D) in central Monterey Bay, Calif. N-5 and N-6 were directly east of N-4, 0.5 and 1 km, respectively.

A third, but much shorter transect (40 m long) was located along a flat ridge in the head of the Monterey Submarine Canyon (Figure 1). Four stations were established at 10 m intervals and at a constant water depth of 14 m. One end of the transect (station D) was highly disturbed by the slumping of sediment down an adjacent terrace wall. No sediment slumping occurred along the opposite end of the transect (station A) (see Environmental Setting section). The movement of sediment by slumping was measured by periodic depth soundings along the terrace wall and by diver observations and measurements at permanent underwater stations. Divers measured the distance from the bottom to the tops of the steel station rods at monthly intervals from May to November 1972. Periodic visual observations of station migrations and algal accumulations proceeded until mid-1974.

All samples and field observations were made by divers using scuba. Routine samples were taken with diver-held can corers (length = 17 cm; area = 0.018 m^2) and were washed over a 0.5 mm screen in the laboratory. Eight replicate can cores were usually taken in a haphazard fashion (Fager 1968) at each station on each sampling date. The can corers were 3-lb coffee cans with both ends removed. Animal and sediment loss were prevented by water-tight snap-on plastic lids. Residues were fixed in 4% formaldehyde and transferred to 70% ethanol after sorting. The macrofaunal invertebrates were identified to species (i.e., nematodes, foraminiferans, and copepods were excluded).

A long, diver-operated corer (length = 60 cm; area = 0.018 m^2) was used to document the vertical distribution of organisms within the sediment at southern sandflat stations in 9, 18, and 30 m of water during August 1972. To maintain the strata and minimize animal movement through them, the corers were held horizontally after sample procurement. Some cores were sectioned immediately in the boat and others were sectioned within an

hour at the laboratory. Biomass was calculated from samples taken with a hydraulic suction dredge (Brett 1964) in August 1972. Vertical layers were excavated from a 0.25 m^2 cylinder and collected separately in 1 mm mesh bags. Animals were weighed after being removed from 70% ethanol and air-dried for 10 min. These weights were converted to grams of organic material with the conversion factors of Lie (1968).

Animals swimming near the bottom were sampled with a funnel trap, an inverted funnel (20 cm in diameter) with the spout leading up and into a holding jar. Legs held the traps within several centimeters of the bottom. These traps were set periodically throughout the entire year, primarily at M-2 (Figure 1; 9 m).

The availability of polychaete larvae was estimated by the settlement of larvae into plastic collecting jars. The jars were wide-mouth gallon containers (mouth diameter = 10.5 cm; volume = 4.5 l) held vertically in a rack at a height of 1 m from the bottom. Jars were collected at 14-day intervals from September 1972 to June 1975 at station M-4 (Figure 1; 18 m). No sediment was placed in the jars, but a 1 or 2 cm layer of seston accumulated during each interval. The jars were covered with a galvanized mesh (1 cm square) to prevent the entrance of fish. The jar contents were washed over a 0.25 mm screen and preserved in 4% formaldehyde. Postsettlement polychaetes were identified to species.

Diver observations of sediment movements and current patterns were frequent. Direct measurements of wave height and wave period were also made in the northern bay from September 1971 to February 1973. They were recorded by the Corps of Engineers from Santa Cruz Pier approximately 18 km from the study area. Although wave heights were generally greater in the central bay, the seasonal patterns were similar throughout the bay.

Feeding and burrowing observations were made in the laboratory and gut contents were examined under a compound microscope. If an animal contained only sediment, it was called a deposit feeder. Some deposit feeders also preyed on other infauna in an aquarium.

ENVIRONMENTAL SETTING

Central Monterey Bay is characterized by high-energy beaches (sensu Clifton et al. 1971) that have a relatively gentle seaward slope and a well-developed winter berm. The most distinct physiographic feature is the large Monterey Submarine Canyon (Figure 1). Prevailing wind and wave direction is from the northwest. Wave refraction in relation to bottom topography concentrates wave energy on the northern sandflat and disperses wave energy in the canyon head and along a portion of the adjacent southern sandflat. Width of the breaker zone and wave height increase dramatically to the north and south of the canyon head (Gordon 1974).

Wave-generated bottom currents have primary control over the sedimentary environment of a beach. Clifton et al. (1971) gave a detailed description of wave-generated depositional structures in the high energy-nearshore environment along the southern coast of Oregon. The same major depositional structures and zones were present in central Monterey Bay. The relative position of the nearshore and offshore is illustrated in Figure 2. The bulk of the faunal sampling and other field observations was performed in the offshore area (Figure 2).

Strong longshore tidal currents can produce lingoid and undulatory small ripples (Reineck and Singh 1973) that trend perpendicular to the ripples produced by oscillating wave-generated currents. Both types were observed at the stations in 18 m of water and deeper, and often resulted in a complicated maze of discontinuous ripple crests. In shallower water, wave-generated currents were more intense and dominated the depositional structure. They produced ripple crests in the fine sand that were more or less continuous and normal to the direction of wave arrival. During periods of large winter swell, conditions at the 9 m station were very similar to those described for the "outer planner facies" of the nearshore by Clifton et al. (1971). Here, ripple marks were obliterated by wave currents and the sediment moved in sheet flow. Fager (1968) observed similar "miniature sandstorms" on the sandflats adjacent to the Scripps Institution of Oceanography in southern California.

The bottom threshold velocity of sediment movement is highly dependent on water depth. Given the narrow range of grain size distributions among the sandflat stations (Table 1), the predominant factors controlling the threshold of sediment movement along the sandflat transects were undoubtedly water depth, wave height, and wave period (Komar 1976). Since unidirectional longshore currents had a decreasing impact on the surface sedimentary structures with decreasing

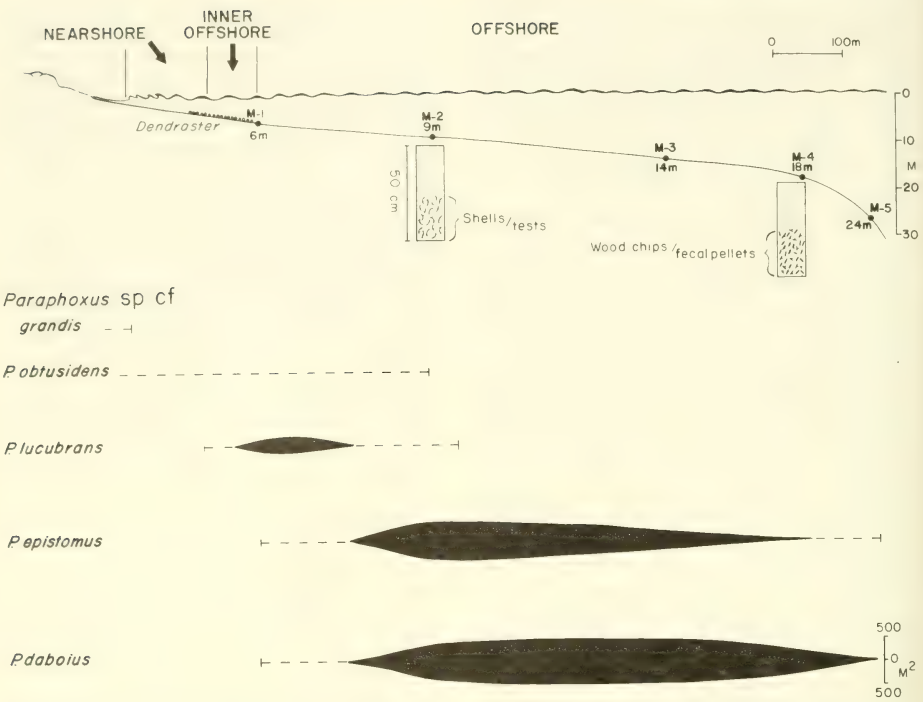


FIGURE 2.—Schematic profile of the beach along the southern transect showing sediment profiles from long cores and the zonation of paraphoxid amphipods in Monterey Bay, Calif.

TABLE 1.—Characteristics of the surface sediments along southern (M) and northern (N) transects in Monterey Bay, Calif. (mean ± 95% confidence limits).

Station	Depth (m)	*n* samples	Md (ϕ)[1]	% fine sand (0.250-0.062 mm)	% silt (<0.062 mm)	Coefficient sorting[2]	% organic carbon
M-1	6	6	2.93±0.30	94.4± 5.4	1.0±1.3	0.44±0.03	0.08±0.012
M-2	9	11	3.27±0.04	91.4± 3.6	8.1±3.8	0.47±0.04	0.13±0.020
M-4	18	7	3.39±0.05	93.3± 1.5	6.2±1.5	0.38±0.02	0.10±0.050
M-5	24	7	3.53±0.05	87.6± 2.0	10.8±1.6	0.43±0.02	0.18±0.020
N-2	9	3	3.04±0.20	96.1± 7.0	1.0±0.1	0.42±0.20	—
N-3	18	3	3.15±0.03	95.5± 3.6	1.3±1.9	0.42±0.03	—
N-4	24	3	3.06±0.10	88.9±14.0	2.0±0.3	0.54±0.30	—

[1] $\phi = -\log$ (median diameter).
[2] Folk and Ward (1957); higher coefficient equals poorer sorting.

water depth, the primary sediment movements were caused by waves intercepting a shoaling bottom.

An increase in wave height and a decrease in wave period both cause an increase in the velocity of sediment movement (Komar 1976). As a result, winter wave conditions should cause the greatest sediment motion (Figure 3). Hundreds of dives and years of qualitative observations of wave activity indicated a strong gradient in substrate movement with changing depth along the sandflats as well as considerably greater sediment motion dur-

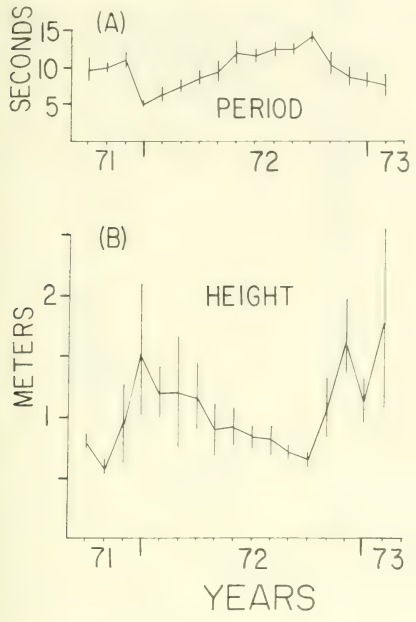


FIGURE 3.—Monthly wave periods (A) and heights (B) during 1971-73 at the Santa Cruz pier in northern Monterey Bay, Calif. (means and ranges).

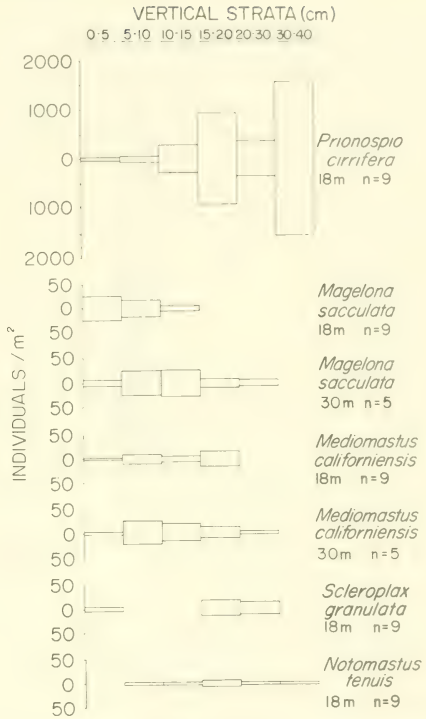


FIGURE 4.—Vertical distribution of invertebrate species living deep in the sediment in Monterey Bay, Calif. (mean per layer based on n cores 50 cm long).

ing the late fall and winter months. These observations are consistent with theoretical expectations (Komar 1976).

Examination of the residue retained by the 0.5 mm mesh screen during the processing of vertical strata from the long cores revealed additional characteristics of the depositional environment. At the 9 m station, strata below 25 cm contained broken tests and spines of the sand dollar *Dendraster excentricus*, broken mollusc shells, and rounded, olive-green silt stones. The surface stratum (top 25 cm) was homogenous fine sand (Figure 2). Similar stratification was observed by Howard and Reineck (1972) in the upper offshore of a low-energy beach along Sapelo Island, Ga. This concentration of shells and tests probably resulted from physical winnowing or reworking during severe storms.

Long cores from 18 and 30 m had no shell/test strata. Instead, there was a concentration of woody chips of terrigenous, riverine origin and a high density of large oblong fecal pellets (1 mm length) below 25-30 cm in the sediment (Figure 2). The fecal pellets belonged to the deposit-feeding capitellid polychaete *Notomastus tenuis*, which lives deep in the sediment column (Figure 4). Although fecal pellets were produced in situ, the wood chips had been deposited on the surface and were either buried by subsequent deposition or by the biological reworking of the upper sediment layers. Many large deposit feeders burrowed to a depth of 20-30 cm (Figures 4, 5, 6). Nevertheless, this deposit would not persist at the shallower depths of stronger physical winnowing.

In summary, surface ripple mark patterns, the composition of deep sediment layers, frequent field observations, and theoretical predictions indicate a unidirectional gradient in substrate motion highly dependent on depth.

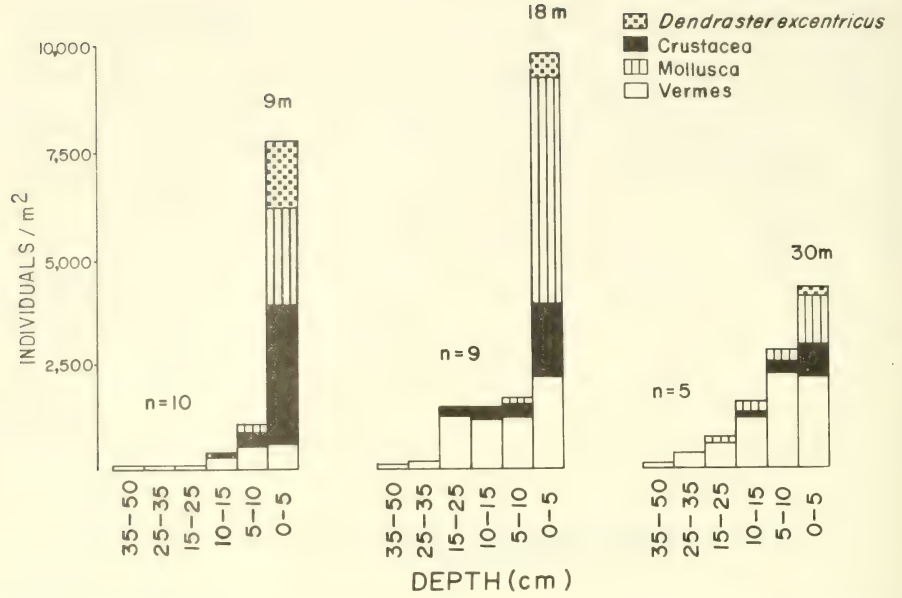


FIGURE 5.—Mean number of individuals per square meter per long core layer in n long cores in Monterey Bay, Calif. Vermes are 90% polychaetes and include enteropneusts, phoronids, oligochaetes, and nemerteans.

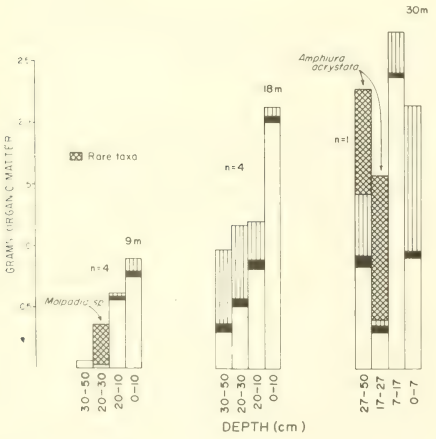


FIGURE 6.—Mean biomass of animals per suction dredge layer in Monterey Bay, Calif. (except at 30 m, where n = 1). Rare taxa indicated. See Figure 5 for bar legend.

Sediment movements in the canyon head included unidirectional down-canyon creeping and slumping as well as oscillatory movements. Diver observations and measurements at permanent bottom stations indicated a general shoaling of shallow (5-15 m) terrace walls and an accumulation of drift plants (primarily *Ulva lobata, Macrocystis pyrifera, Zostera marina*) during the summer and early fall. Slumping of terrace walls and down-canyon flushing of channels were coincident with the first fall storms and continued through the winter (see Arnal et al. 1973). The same seasonal cycle of sediment accumulation and flushing was observed at the heads of the Scripps and La Jolla Submarine Canyons (Shepard and Dill 1966).

One of the major slumping events occurred at the shoreward end of the flat canyon ridge. Sediment creeped down the terrace wall (5-14 m), across the ridge (14 m), and into the deeper canyon channel (25 m). The slumping was evidenced by a change in the position of the terrace wall, the exposure of consolidated mud outcrops on the ter-

race after the fall storms, and the down-canyon movements of station markers along this part of the ridge. The change in the terrace wall position was reflected in a 1 or 2 m increase in the depth of a midwall reference station and in the shifting of the wall base closer to the permanent stations on the ridge. The station markers (rods) at station C and especially D were also moved and slanted in a down-canyon direction. Furthermore, a large ship anchor, dropped in slightly deeper water below station D, moved about 10 m in the same down-canyon direction (Arnal et al. 1973). In contrast, the station stakes at stations A and B remained in a vertical position and did not move. The slumping of the terrace wall during the fall and winter was observed in other years and in other parts of the canyon head as well (Arnal et al. 1973; pers. obs.).

The four ridge stations (A-D) were established along a gradient of substrate motion. Station D was nearest to the slump zone and station A was farthest from the terrace wall, where there was no evidence of sediment slumping. The animals were sampled once along the transect in December 1972. Although there were no significant differences in the median diameter of the sediment and the sorting coefficients among the four stations ($P>0.1$; Kruskal-Wallis test, Conover 1971), the surface sedimentary structures indicated the persistence of the substrate disturbance gradient from October to December. During this entire period, the sandy sediment was well consolidated and formed parallel ripple marks at stations A and B, but was poorly consolidated and had no ripple marks at stations C and especially D (the area of creeping).

This change in substrate consolidation and ripple mark patterns was not caused by changes in tidal or oscillatory-wave currents. Tidal and longshore currents did not vary along the 40 m transect. Moreover, since oscillatory bottom currents primarily depend on the grain size, water depth, wave height, and wave period (Komar 1976), which were all constant along the transect, the bottom threshold of sediment movement by these currents did not differ among the ridge stations. Therefore, the slumping gradient cannot be quantified in terms of resuspended material or bottom current velocity. On the other hand, poorly consolidated sandy sediments characterized all the slump areas we observed in the canyon head and were also documented in a large slump near the Scripps Canyon in southern California (VanBlaricom 1978; pers. obs.). These slumping events are extremely difficult to quantify because they have never been witnessed (see Shepard and Dill 1966). Nevertheless, the observations and indirect measurements indicate a unidirectional gradient of substrate motion related to the distance from slumping canyon walls and channeling topography. Stations A (low movement) and D (high movement) represent the ends of this gradient.

OFFSHORE ZONATION PATTERNS ALONG THE SOUTHERN SANDFLAT

The gradational nature of the invertebrate assemblages was apparent from the changes in species abundance along the offshore transect (Table 2). The crustaceans were the numerically dominant group at the 6 and 9 m stations (M-1 and M-2). The density of crustacean species and individuals was highest at 9 m (Figures 7, 8). Six of the seven most abundant species at this station were crustaceans (Table 2). The number of crustaceans decreased steadily seaward of 9 m. The 14 m station was a distinct transition zone between a shallow offshore crustacean assemblage and a deeper polychaete assemblage (Table 2; Figure 7).

The 6 m station was located at the seaward edge of a large bed of *Dendraster excentricus*. The width of the sand dollar bed increased with distance from the canyon head. It was approximately 40 m at the southern sandflat transect (Figure 1) and >75 m wide 2 km to the south. Merrill and Hobson (1970) described a protected open coast *D. excentricus* bed which was similar to the local situation.

Crustacean Zone

Crustaceans

The abundant animals of the shallow-water zone were small, actively burrowing, deposit-feeding amphipods and ostracods (Table 2). The amphipods belonged to three typically sand-dwelling families, Oedicerotidae, Phoxocephalidae, and Haustoriidae, and the ostracods to the Philomedidae. Each family was represented mainly or exclusively by one genus of several species and each species was often found within distinct depth limits.

The genus *Eohaustorius* contained the only representatives of the subfamily Haustoriinae on this coast (Bousfield 1970). Temporal variations in *Eohaustorius sencillus* and *E. sawyeri* were relatively complementary at the 6 m station and may

TABLE 2.—Ten most abundant species at each station along southern transect in Monterey Bay, Calif. Data are number square meter ± 95% confidence limits and percent frequency of occurrence in *n* samples in parentheses. × = species that ranked 11-17 in abundance; B = semipermanent burrow; T = tube dweller.

	Crustacean zone			Polychaete zone	
Species	M-1, 6 m *n* = 108	M-2, 9 m *n* = 107	M-3, 14 m *n* = 30	M-4, 18 m *n* = 141	M-5, 24 m *n* = 28
Crustacea:					
Euphilomedes longiseta	854±209 (81)	397±110 (62)			
Eohaustorius sencillus	351±105 (60)	1,234±165 (100)	333±127 (80)		
Paraphoxus lucubrans	298± 72 (68)				
E. sawyeri	182± 50 (58)				
Synchelidium spp.	143± 44 (59)				
P. obtusidens	66± 21 (31)				
Euphilomedes oblonga		1,064±204 (87)	513±220 (93)		
P. daboius		799±176 (94)	970±209 (100)	402± 61 (91)	〃
P. epistomus		722±116 (98)	320± 94 (97)		
E. carcharodonta		397±116 (76)	〃	〃	
Mollusca:					
Olivella pycna	309±479 (37)				
Tellina modesta	55± 17 (43)	738±182 (93)	132± 61 (63)	722±171 (68)	309±121 (93)
Mysella aleutica		386±110 (81)	×		
Prototheca staminea			×	105± 39 (44)	〃
Polychaeta:					
Prionospio pygmaea T, B	110± 50 (19)	〃	149± 72 (60)	237± 50 (84)	573±342 (68)
Scoloplos armiger	105± 33 (56)				
Armandia bioculata		276±133 (32)			
Magelona sacculata B	×	237± 72 (61)	303±171 (80)	1,174±231 (94)	628±220 (100)
Amaena occidentalis B		×	204± 72 (87)	138± 39 (57)	276±110 (68)
Mediomastus californiensis		×	182± 66 (80)	331± 50 (93)	1,053±231 (96)
Northria elegans T		×	116± 44 (67)	242± 28 (96)	435± 94 (100)
Lumbrineris luti B				226± 28 (94)	242± 50 (93)
P. cirrifera T, B				193± 99 (55)	303±132 (89)
Nephtys cornuta				×	325±105 (93)
Edwardsia sp. (Anthozoa) B				〃	150± 62 (80)

indicate a well-defined boundary between the two populations (Figure 9). No *Eohaustorius* were captured in funnel traps, indicating that much of the life history occurs on or within the sediment.

The genus *Paraphoxus*, in contrast to *Eohaustorius*, has a wide depth distribution in Monterey Bay (Barnard 1960). Four species occurred along the subtidal transect in much greater densities than populations from deeper portions of the bay (Barnard 1960; Hodgson and Nybakken 1973) and in more well-defined zones (Figure 2). A fifth species was the intertidal *Paraphoxus* sp. cf. *grandis*, a new species (Slattery in prep.).

There is an obvious relationship between certain morphological characteristics and the depth zonation of *Paraphoxus* spp. Larger species reached their peak abundance in shallower water (Table 3). *Paraphoxus* sp. cf. *grandis* and *P. obtusidens* were giants relative to the other three species (Table 3). This large size may be an adaptation to strong sediment motion (Sameoto 1969; Fincham 1971). In contrast, *P. epistomus* and *P. lucubrans* were more streamlined and slightly larger than the deepest species, *P. daboius*. *Paraphoxus daboius* was small and had poorly developed eyes (Table 3). It lived in the calmest water (i.e., deepest) and finest sediment and was the only peracaridean crustacean commonly found below 5 cm in the long cores. *Paraphoxus* were captured by the funnel traps (Table 4).

Euphilomedid ostracods were among the most abundant crustaceans (Table 2). They occasionally occurred in funnel traps (Table 4). In contrast, cumaceans were not abundant on the bottom (Table 2), but were numerous in funnel traps (Table 4). A number of other rare bottom dwellers were also abundant in the funnel traps, including the oedicerotid amphipods *Synchelidium shoemakeri, Synchelidium* spp., and *Monoculodes spinipes*; other amphipods *Atylus tridens, Tiron biocellata*, and *Megaluropus longimerus*; and a number of mysids (Table 4).

No general correlation exists between swimming tendency and species zonation within the crustacean zone. Although more active *Paraphoxus* species were found in shallow water, nonswimming *Eohaustorius* spp. lived at the same depths. Moreover, the cumaceans and oedicerotid amphipods were active swimmers (Table 4) and occurred in relatively low numbers throughout the crustacean zone. On the other hand, there were distinct morphological patterns suggesting greater swimming among shallower species within particular groups (i.e., *Paraphoxus* and *Euphilomedes* species); however, these groups and others may enter the water column for very differ-

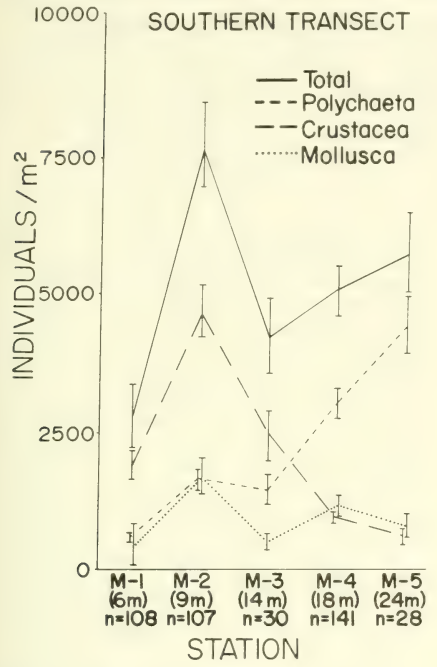


FIGURE 7.—Mean number of individuals per square meter and 95% confidence limits of major groups along the southern transect in Monterey Bay, Calif. (estimates based on n can cores).

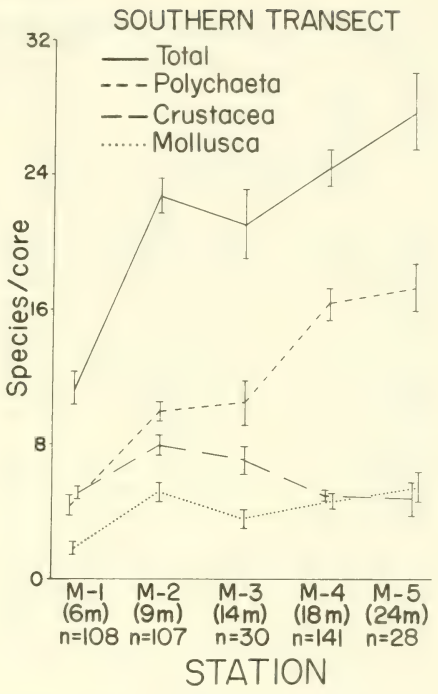


FIGURE 8.—Mean number of species per can core (0.018 m²) and 95% confidence limits of major groups along the southern transect in Monterey Bay, Calif.

ent reasons (e.g., mating, food, substrate movements). Despite these differences, almost all the crustaceans in the crustacean zone were active, free-burrowing species and few inhabited tubes.

Other Animal Groups

The polychaetes were much less abundant than crustaceans in the crustacean zone (Table 2; Figure 7). *Scoloplos armiger, Chaetozone setosa, Nephtys caecoides*, and *Dispio uncinata* were the most characteristic species at the shallowest station (M-1). *Prionospio pygmaea* and *Magelona sacculata* maintained highly ephemeral populations near the surf zone (see Seasonal Patterns). The uncommon onuphid *Onuphus eremita* was only encountered at 6 m (M-1). In general, the more frequent members of the polychaete as-

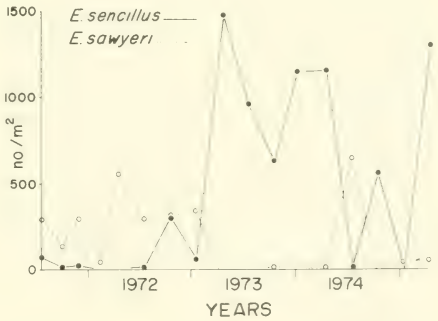


FIGURE 9.—Complementary temporal variations of *Eohaustorius sencillus* and *E. sawyeri* at M-1 (6 m) in Monterey Bay, Calif.

TABLE 3.—Gradation of adult morphological characters in the five species of paraphoxid amphipods in Monterey Bay, Calif.

Character	*Paraphoxus* sp. cf. *grandis*	*P. obtusidens*	*P. lucubrans*	*P. epistomus*	*P. daboius*
Depth of dispersion center	Intertidal	6 m	≥6 m	9 m	14 m
Mean size (mm) mature females (±SD)	15±2.5	12±2.2	4.5±0.8	3.7±0.4	2.8±0.2
Ratio of eye diameter to body length	1:35	1:39	1:17	1:33	1:56
Ratio of inner[1] to outer ramus of uropod III	1:1.09	1:1.04	1:1.1	1:1.5	1:4.2
Number of individuals measured	10	10	20	20	20

[1]Higher ratio indicates more foliose uropod used in swimming.

TABLE 4.—Abundance of crustaceans caught in funnel traps at station M-2 (9 m) in Monterey Bay, Calif. (410 trap days).

Species	No. trapped	Species	No. trapped
Amphipods:		Cumaceans:	
Synchelidium shoemakeri	160	*Diastylopsis tenuis*	57
Paraphoxus daboius	79	*Lamprops carinata*	35
Atylus tridens	66	*Hemilamprops californica*	27
Tiron biocellata	40	*Mesolamprops bodegensis*	25
Monoculodes spinipes	40	*Cyclaspsis* spp.	9
P. epistomus	11	*Anchicolorous occidentalis*	4
Megaluropus longimerus	1	Mysids:	
Ostracods:		*Neomysis kadiakensis*	550
Euphilomedes carcharodonta	12	*Acanthomysis* spp.	250
E. longiseta	7	Others	50
E. oblonga	5		

semblage at M-1 were mobile deposit feeders. The most abundant polychaetes at M-2 (9 m) were species that maintained larger populations in deeper water. The one exception, *Armandia brevis*, had a low frequency of occurrence (Table 2), was highly opportunistic, and primarily lived in more protected areas (Oliver 1979).

Polychaete Zone

The polychaete zone (Table 2) was characterized by animals that require a more stable substratum to establish and maintain burrows and tubes. Most of the polychaetes living exclusively in the shallow crustacean zone did not have permanent tubes or burrows (Table 2). This was true of all the crustaceans. The gradual change in ripple mark and vertical sedimentary structure discussed previously reflected this increase in substrate stability. There were several other distinct visual changes between the two zones. The most conspicuous were the increase in burrow openings and tube fragments and the density of large siphons of the goeduck, *Panopea generosa*, which was first encountered in the transition area (14 m).

Polychaetes

The polychaetes *Magelona sacculata* and *Nothria elegans* were abundant at the deeper stations (Table 2). The onuphid *N. elegans* lived in a vertical tube constructed of clean sand. Laboratory observations and gut contents indicated that *N. elegans* was a surface-deposit feeder, scavenger, and predator. *Magelona sacculata* lived in a burrow and was a surface-deposit and suspension feeder. The gut contents of 25 *M. sacculata* were mainly amorphous organic matter with very little sand.

Many other polychaetes were generally more abundant in deeper water. These included the spionids *Prionospio cirrifera* and *P. pygmaea* and the large terebellid *Amaeana occidentalis* (Table 2). *Amaeana occidentalis* constructed a burrow with a mucus-impregnated wall and was capable of extensive burrowing activity in the laboratory. The mouth was often positioned a centimeter or more below the substrate surface with the tentacles extended through the sediment and into the overlying water. The gut contents of *A. occidentalis* and *Prionospio* spp. were similar to those of *M. sacculata*. Apparently, they scrape fine material from the sediment-water interface and catch suspended particles.

In general, a higher proportion of animals was found in lower vertical sediment strata from the polychaete zone (>14 m depth) compared with the crustacean zone (Figures 5, 6). This was expected due to the greater number of tube- and burrow-dwelling inhabitants. Coincident with this increase was an increase in known or suspected commensal or symbiont animals. These included the pinnotherid crabs *Scleroplax granulata* (Figure 4) and *Pinnixa franciscana* and several species of polynoid polychaetes. Although Day (1967) described the paraonid polychaetes as shallow surface burrowers, almost half of the individuals of the three local species (*Aricidea suecica*, *Aedicira pacifica*, and *Paraonides platybranchia*) were found below 10 cm in the sediment (9 individuals in 0-10 cm and 7 in 10-20 cm).

Several rather small species also burrowed deep into the sediment. The capitellid polychaete *Mediomastus californiensis* was generally <1 cm long after preservation and was found throughout the sediment column (Figure 4). Additionally, the

small (<1 cm long) *Prionospio cirrifera* was found as deep as 30-40 cm in the sediment (Figure 4). It was the most abundant polychaete from the long cores at the 18 m station (Figure 4) and yet ranked only seventh in abundance, when the top 10 cm of the sediment was considered separately. Spionids have ciliated feeding palps and dorsal gill filaments. They generally live in mucus-lined burrows or sand tubes and feed on, or just above, the bottom surface (Hartman 1941). Perhaps *P. cirrifera* inhabits the burrows of thalassinid shrimps in a manner similar to the phoronid worm *Phoronis pallida*. In Bodega Bay, Calif., *P. pallida* is found deep in the sediment in association with *Upogebia pugettensis* (Thompson 1972). The lower portion of the phoronid tube is constructed of relatively coarse sand and the distal end is composed of fine black sediment where the tube passes through the burrow wall of *U. pugettensis*. The tube is oriented normal to the shrimp burrow such that the lophophore can be extended into the burrow for feeding and respiration (Zimmer[2]). Coincidentally, the highest concentration of *P. cirrifera* per vertical stratum (175) was found deep (30-40 cm) in the only core that contained a large thalassinid, *Callianassa* sp.

It is important to note that these vertical patterns were not artifacts resulting from migration down the core or from physical disturbance. Corers were oriented horizontally while out of water and quickly cut by extruding the core from the corer bottom. Moreover, animals that were known to live very near to the sediment-water interface were not displaced (e.g., small bivalves, crustaceans, and *Nephtys cornuta*).

Other Animal Groups

Although the density of crustaceans was very low in the polychaete zone (Figure 7), the number of tube-dwelling forms was greater (e.g., *Ampelisca* and *Photis* species). Variations in the number of individuals and species of bivalve molluscs (Figures 7, 8) were due to periodical heavy settlement along the entire transect. Juvenile mortality was almost complete and very few specimens were observed that were larger than a few millimeters. The same observation was made by Muss (1973) in the Øresund in Denmark. The most abundant local bivalves were *Tellina modesta* and *Mysella aleutica* (Table 2). The distribution of *T. modesta* was correlated with the percentage of silt in shallow-water sediments by Barnard (1963). Large individuals were observed in the northern bay and in Moss Landing Harbor, where the fine sediment fraction was greater than that along the transects. There were also high numbers of small (1 mm) juvenile bivalves present in the surface strata of the long cores (Figure 5); however, most of the biomass of molluscs in the lower, hydraulically dredged strata was due to a few large individuals of *Solen sicarius* and *Macoma* spp. (Figure 6).

Ophiuroid communities are generally found at depths ranging from 45 to 90 m in southern California (Barnard and Ziesenhenne 1961). Large individuals of *Amphiura acrystata* were found deep in the substrate at the 24 m station. The animal's oral disc was usually 10-15 cm below the surface and its arms extended through the sediment into the water column. All observed individuals appeared to be suspension feeding. The density of *A. acrystata* was $<1/m^2$ at the 24 m station, but increased to 1 or $2/m^2$ south of the study area.

NORTHERN SANDFLAT

The northern sandflat received larger waves and the bottom surge was consistently greater than that along the southern sandflat. The theoretical difference in relative wave energy reaching both beaches was estimated from a detailed wave refraction diagram.[3] Assuming wave arrival from the northwest and wave period of 14 s, the total energy reaching the southern transect is only three-quarters of that arriving at a comparable segment of the northern beach. The southern stations also had finer sediment compared with the same northern depths (Table 1). During winter storms, wave heights in the northern area were often more than a meter higher than those at the southern study site. These differences only occurred close to the canyon in the vicinity of the sampling transects and were corroborated by hundreds of scuba diving observations of substrate motion and wave swell on the two sandflats.

If the primary control of the offshore zonation pattern is due to wave-induced substrate motion,

[2]R. Zimmer, Professor, Biology Department, University of Southern California, Los Angeles, CA 90007, pers. commun. June 1973.

[3]U.S. Army Corps of Engineers wave refraction diagrams 14-51-1, 1948.

then faunal zones should be shifted into deeper waters by an increase in wave activity. The difference in wave energy arriving at the two sides of the canyon allows a partial test of this hypothesis. As predicted, the animal zones described on the southern sandflat were wider and shifted toward deeper water on the northern sandflat (Figures 7, 10). Density of crustaceans was highest in 18 m of water, the transition zone was wider, and polychaetes did not increase in number until 30 m (Figure 10). Nevertheless, the shape of the curves in Figures 7 and 10, and thus the gross zonal patterns, were remarkably similar. The abundant species were the same on both sides of the canyon, but the rank orders of abundance were not identical (Oliver 1979). Abundance of the numerically dominant crustaceans and the total number of crustaceans was significantly higher along the northern transect (Figures 7, 10). Presumably, this increase was related to the extension of the crustacean zone into deeper water.

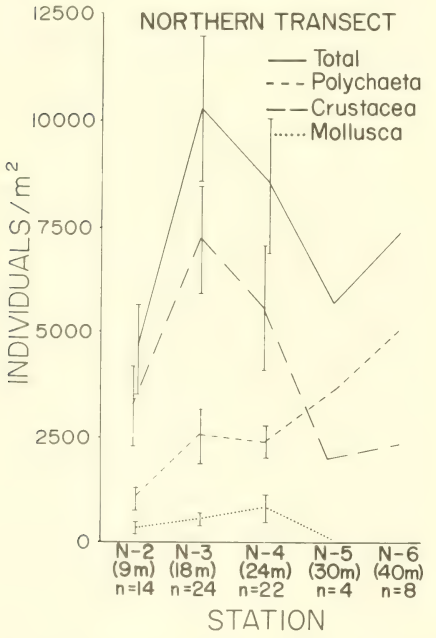


FIGURE 10.—Mean number of individuals per square meter and 95% confidence limits of major groups along northern transect in Monterey Bay, Calif. N-5 and N-6 were only visited once.

The predicted effect of increased wave activity on the infaunal zonation was also observed on the zonation of the sand dollar bed. During moderate to heavy sea states, the outer edge of the bed was in 6 m on the southern and in 9 m of water on the northern sandflat. In addition, the bed was more than 30 m wider along the northern transect. Therefore, the greater width and seaward depth limits of the sand dollar bed were also associated with stronger wave swell.

CANYON RIDGE TRANSECT

Faunal changes along the canyon ridge transect provide further evidence for the relationship between benthic community zonation and substrate motions. The ridge stations (A through D) traversed a substrate movement or disturbance gradient at a constant water depth of 14 m. Therefore, a number of other environmental factors that changed with water depth along the sandflats did not vary along the ridge transect. These included light, temperature, resuspension and settlement of food particles, and the zonation of predatory demersal fish (see Discussion). On the other hand, there was a distinct gradient of substrate movement along the sandflats as well as along the canyon ridge. The type of sediment movement, however, was rather different. The primary substrate movements along the sandflats were caused by wave-generated, oscillating bottom currents, which became greater with decreasing water depth. Water depth was constant along the ridge. This substrate disturbance gradient was caused by a unidirectional (down-canyon) creeping of sediment which was greater at stations located nearer to the terrace walls and channels (i.e., stations D and C) (see Environmental Setting).

Despite these differences, benthic community zonation was similar along the sandflat and canyon ridge transects. The similarity is partially illustrated by the abundance of polychaetes and crustaceans (Figure 11). The most striking parallels, however, were in the distributions of individual species (Oliver 1979). Species that were highly characteristic of the shallowest sandflat stations (e.g., *Scoloplos armiger, Dispio uncinata, Onuphus eremita, Olivella pycna, Euphilomedes longiseta*) were found at stations D and C along the ridge (zone of sediment slumping). Species that were most abundant at intermediate sandflat depths were found at intermediate ridge stations, C and B (e.g., juvenile *Dendraster excentricus,*

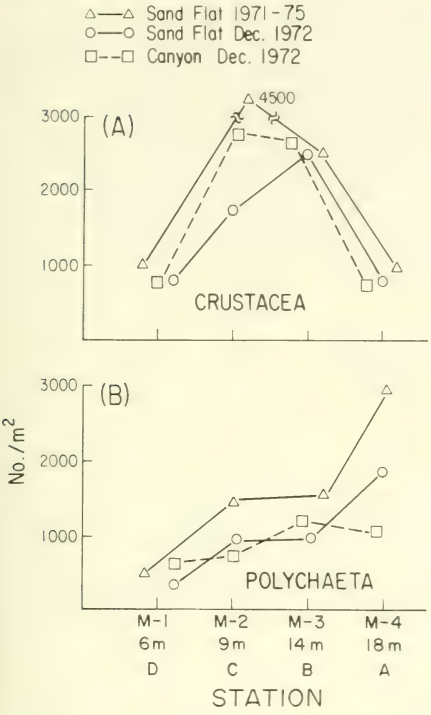


FIGURE 11.—Variations in abundance of crustaceans and polychaetes along the canyon ridge (A-D) and sandflat transects (M) in December 1972, and along the sandflat from 1971 to 1975 in Monterey Bay, Calif.

Eohaustorius sencillus, Euphilomedes carcharodonta). Finally, several polychaetes (*Nothria elegans, Amaeana occidentalis, Lumbrineris luti, Magelona* spp.) that were common in deeper water were most abundant at ridge stations B and especially A (farthest from sediment slumping).

There were only a few statistically significant correlations between the abundance of individual species along the sandflat and canyon transects ($P<0.05$). Since the correlations involved four pairs of stations, there were just 2 degrees of freedom in determining the significance of a product-moment correlation coefficient (Snedecor and Cochran 1967). With 2 degrees of freedom, a significant ($P<0.05$) coefficient must be at least $r = 0.95$. However, there were more positive correlation coefficients computed for the individual species than expected by chance alone. Eighteen of the most abundant 23 species (those inhabiting both transects at >1/core) had positive coefficients. Assuming no correlation between the two transects (i.e., independence), the probability of 18 positive correlation coefficients is 0.019 (sign test, Snedecor and Cochran 1967). The probability is less when only the species with relatively distinct zonation patterns are considered ($P<0.01$). The average correlation coefficient among these species is 0.54 ± 0.12 (95% CL). Therefore, although few individual species showed a statistically significant correlation in abundance along the sandflat and canyon transects, there was a significant trend in positive correlation when the abundant species were considered together.

In summary, benthic community zonation along the gently sloping sandflats (6-18 m) was similar to the zonation along a constant depth transect on the canyon ridge (14 m). This similarity was observed despite differences in substrate disturbance (oscillating vs. unidirectional creeping) and transect lengths (almost 1 km vs. 40 m).

SEASONAL PATTERNS

Seasonal changes in polychaete abundance were more regular than those of the crustaceans (Figures 12, 13). The lowest polychaete abundance generally occurred in the late fall and the winter (Figure 12). The most dramatic population de-

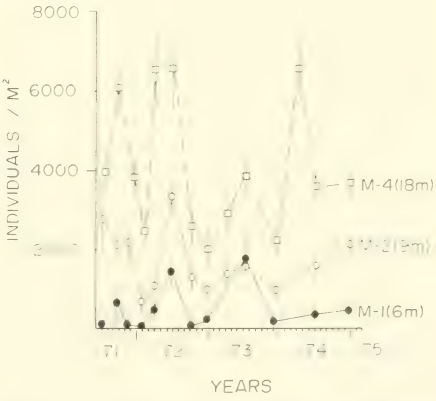


FIGURE 12.—Temporal variations in number of polychaete individuals at three depths along the southern sandflat in Monterey Bay, Calif. (means and 95% confidence limits).

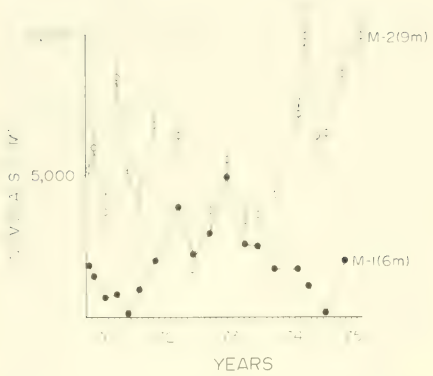


FIGURE 13.—Temporal variations in number of crustacean individuals along the southern transect in Monterey Bay, Calif. (means and 95% confidence limits).

creases, to zero in some cases, were at the shallowest station (Figure 12; M-1, 6 m). Because of the shallow water depth, wave-induced substrate motions were most severe at this station (see Environmental Setting). Furthermore, seasonal substrate movements were greatest during the late fall and winter, when wave heights were large and wave periods short (Figure 3). Therefore, the lowest polychaete numbers were found during that time (late fall and winter) and at the water depth (6 m) corresponding to the greatest substrate motions.

Many environmental factors had a general seasonal trend similar to wave activity. Water temperature, river runoff, and phytoplankton standing stocks also had marked winter-summer variations in Monterey Bay (Oliver et al.[4]). However, wave-induced sediment motion was one of the only seasonal factors that changed with water depth and was, thus, coincident with the depth and seasonal changes in polychaete abundance. The depth-dependent changes in resuspended particulate material are treated in the discussion.

Prionospio pygmaea, Armandia brevis, and *Magelona sacculata* settled into the crustacean zone (M-1 and M-2), but rarely survived to adult size. Their frequency of occurrence at the shallower stations was much lower than it was in deeper water (Table 2). Moreover, the low population abundance during the winter was not simply a result of seasonal changes in larval availability. Although some polychaete species appeared to have a relatively seasonal pattern of larval availability (e.g., *M. sacculata*), the larvae of other species (e.g., *N. elegans* and *P. cirrifera*) were present throughout the year (Figure 14).

The seasonal peaks in polychaete abundance in deeper water (M-4, 18 m) were largely due to the

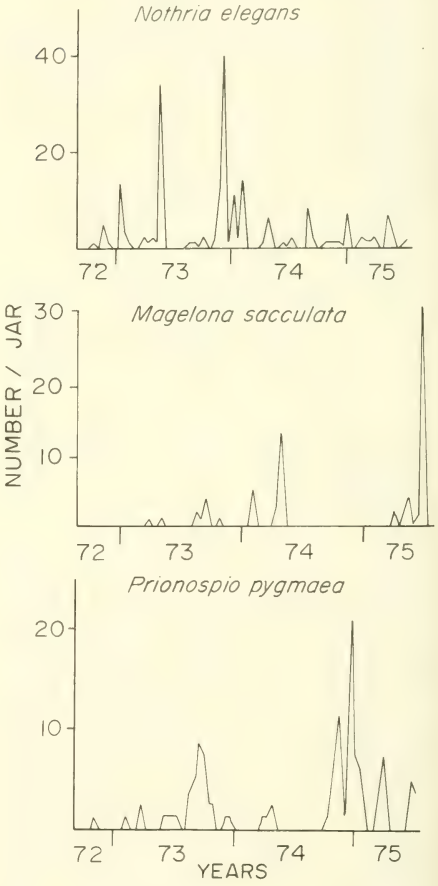


FIGURE 14.—Abundant sandflat polychaetes collected in larval settling jars at the 18 m station (M-4) in Monterey Bay, Calif.

[4]Oliver, J. S., P. N. Slattery, L. W. Hulberg, and J. W. Nybakken. 1977. Patterns of benthic succession after dredging and dredge material disposal in Monterey Bay, California. U.S. Army Corps Eng. Waterways Exp. Stn., Tech. Rep. 0-77-27, 186 p.

settlement of *M. sacculata*. The correlation of the abundance of *M. sacculata* with the total number of polychaetes at M-4 was highly significant ($r = 0.71$; $P<0.001$). *Magelona sacculata* generally accounted for about one-quarter of the polychaete numbers at M-4. As a result, polychaete abundance patterns in deeper water were dominated by seasonal changes in larval availability (Figure 14) and recruitment, and were not clearly related to substrate motions. This correlation between the abundance of *M. sacculata* and the total polychaete numbers decreased in shallower water (M-2, 9 m: $r = 0.34$, $P>0.1$; M-1, 6 m: $r = 0.39$, $P>0.1$).

In summary, seasonal abundance patterns were probably affected by a number of environmental factors including seasonal reproductive cycles and substrate motions. The recruitment or survival of polychaetes was lowest at the time of year and water depth of maximum substrate motions. Hence, the zonation of polychaetes in the crustacean zone was apparently influenced by seasonal changes in wave-induced substrate movements. On the other hand, seasonal variations in crustacean abundance and in deeper living polychaete populations could not be related to sediment motion in a simple manner.

DISCUSSION

The general zonation of benthic invertebrate communities observed in central Monterey Bay is common along much of the temperate open coast of western North America. Carey (1965, 1972), Lie (1969), and Lie and Kisker (1970) observed a high abundance of crustaceans at their shallowest sampling stations and the numerical dominance of polychaetes in deeper areas off Oregon and Washington. Barnard (1963) and VanBlaricom (1978) found the same two zones in southern California and Hodgson and Nybakken (1973) described a comparable pattern in the northern part of Monterey Bay. A similar change from a crustacean- to a polychaete-dominated assemblage was also related to wave exposure by Masse (1972) in the Mediterranean. On the other hand, Day et al. (1971) and Field (1971) did not find a rich crustacean fauna in the "turbulent" zone they described in 3-20 m on the continental shelves of North Carolina and False Bay, South Africa, respectively.

The composition of the fauna along the sandflats was similar to that found at comparable depths in southern California, but the animal density in Monterey Bay was almost a power of 10 greater (compare Table 2 with Barnard 1963). This disparity was greatest in the crustacean zone. The differences are probably related to different sampling methods: diver corers contrasted to the orange-peel grab used in the earlier studies.

None of the previous studies provide convincing evidence for a relationship between community zonation and wave-induced substrate motions. Although the evidence from the present study is descriptive and correlative, it is consistent with many observations. The general hypothesis is that wave-induced sediment movement has a strong influence on community zonation along the subtidal high-energy beach.

Some of the strongest evidence supporting this hypothesis comes from the natural history patterns of the fauna. There was a significant positive correlation ($r = 0.92$, $P<0.05$) between the water depth of a station and the numbers of tube builders, burrow dwellers, and commensal animals. A similar trend emerges when the animals are grouped into mobile and sedentary forms (Figure 15). Apparently, biogenic structures were difficult or impossible to establish and maintain in areas of more intense physical sediment movement. Although wave disturbance might destroy burrows and tubes and dislodge their inhabitants, some adults were tolerant of heavy sediment accumulations and capable of vertical substrate migrations (e.g., *Nothria elegans*). The zonation of polychaetes may be largely determined by the habitat selection of settling larvae (Oliver 1979).

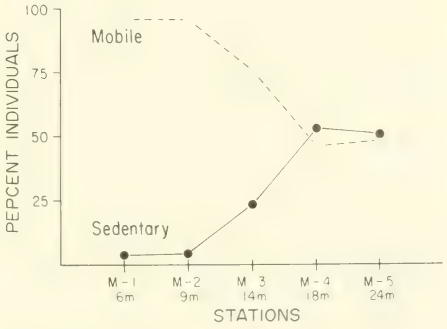


FIGURE 15.—Variations in animal motility patterns along southern sandflat in Monterey Bay, Calif. (percentage of total individuals).

Other natural history patterns also support the relationship between community zonation and substrate motion. In particular, the small peracarid and ostracod crustaceans seem well suited for life in the shifting substrate of the crustacean zone. Their durable chitonous exoskeleton and general activity probably ensure a greater survival relative to many soft-bodied and more sessile forms. Furthermore, their brooding habit and the parturition of large, armoured juveniles undoubtedly increased recruitment success. While no general pattern of crustacean mobility characterized a particular depth, almost all the crustaceans were active burrowers and few maintained a permanent tube or burrow. The lack of dependence on such structures is probably important to the persistence of these large, shallow-water populations. In addition, the most frequently occurring polychaetes in the crustacean zone were also active burrowers that did not live in permanent tubes or burrows.

Variations in zonal patterns along the two sandflats also support the wave-disturbance hypothesis. Wave activity and therefore bottom disturbance were greater along the northern sandflat, where faunal zones were wider and shifted into deeper water. At least one seasonal change in zonation was coincident with an increase in wave activity. The season (late fall and winter) and location (shallowest station, M-1, 6 m) of the greatest wave-induced bottom currents were characterized by the lowest recruitment and survival of polychaetes.

The last source of evidence supporting the hypothesis involves the canyon. While the gradient of substrate motion along the sandflat was caused by waves intercepting a shoaling bottom, the gradient of substrate motion along the canyon ridge transect was caused by unidirectional sediment slumping at a constant depth. Despite these very different types of sediment movement gradients, changes in community zonation along the canyon ridge and sandflat transects were similar. This result negates the importance of several other ecological factors that vary with water depth along the sandflat, but were held constant by the canyon contrast. These include light, temperature, the deposition and resuspension of fine food particles, and the zonation of bottom fish.

The deposition and resuspension of fine particles, which might be used as food, depend upon bottom currents. The strongest bottom currents were caused by wave swell (see Environmental Setting). These oscillatory bottom currents are highly dependent upon water depth and other factors that did not vary along the canyon ridge transect. Thus, while there were probably significant variations in the availability of suspended particles to the different sandflat stations (i.e., their fauna), deposition and resuspension were apparently uniform along the canyon transect.

Demersal flatfish have a zonation that coincides with the zonation of bottom invertebrates. Many species of fish become more abundant with increasing water depth and are more common in the polychaete zone (Table 5). The only species that was numerous in <20 m was the speckled sanddab, *Citharichthys stigmaeus*. Its peak abundance, however, was in 14-18 m and decreased markedly in shallower depths (Ford 1965; Kukowski 1973). Since these flatfish are major predators of sand-bottom invertebrates and they primarily feed by sight (Ford 1965; VanBlaricom 1978; Hulberg and Oliver 1979), active, surface-dwelling crustaceans might be particularly susceptible prey. If this is true, the depth-related increase in bottom feeding fish might account for the correlated decrease in the shallow-water crustaceans. The changes in community zonation along the canyon ridge do not support this idea. Large and highly mobile flatfish can easily patrol the entire length of a 40 m transect.

In summary, trends in the natural history of the animals, changes in zonal patterns along the southern and northern sandflats, seasonal patterns of polychaete recruitment and survival in the shallows, and the similarity between the canyon and sandflat transects support the contention that community zonation is influenced by changes in wave-induced bottom disturbance. Alternate explanations concerning changes in physical sedimentary parameters (Table 1), the availability of suspended food, and the zonation of large flatfish are not consistent with as many observations. One potentially important alternate hypothesis could not be evaluated here. This is the effect of active crustaceans on the settlement and

TABLE 5.—Total number of species and individuals of fish and abundance of the three most common demersal flatfish in otter trawls taken in Monterey Bay, Calif. (from Kukowski 1973).

Item	15 m	36 m
No. species[1]	7.7	13.8
No. individuals	239	359
Citharichthys stigmaeus	33	12
C. sordidus	14	120
Parophrys vetulus	10	33

[1]Mean number caught per 10-min tow with 20 tows at each depth.

early survival of polychaete larvae in the crustacean zone.

The most disruptive wave disturbances were caused by the mass accretion and erosion of the substrate by heavy storm swells. The local sedimentary structures indicated that severe scouring occurred at a water depth of at least 10 m and numerous diving observations revealed significant sediment movement at the deepest study stations. These periodic and catastrophic disturbances are probably more important in maintaining the zonal patterns than the average wave activity of the region. In either case, wave-induced substrate motion undoubtedly prevents the establishment and restricts the activities of many animals and directly or indirectly controls community zonation.

ACKNOWLEDGMENTS

We are grateful to P. Dayton, K. Fauchald, R. Hessler, J. Thompson, and G. VanBlaricom for reading and criticizing an earlier manuscript. This study could not have been completed without the contributions of our friends and colleagues at Moss Landing Marine Laboratories, including R. Christensen, T. Ekhart, R. Fricks, C. Hannan, R. Keegan, L. McMasters, D. Mitchell, E. O'Connor, S. Pace, and many others. Changes in canyon topography were measured by the enthusiastic S. Pace and W. Head. The work was partially supported by the Corps of Engineers in San Francisco (DACW 07-72-C-0060), in Virginia (DACW 72-72-C-0016), and in Vicksburg (DACW 39-74-C-0151). We are indebted to T. Wakeman, R. Yancey, and R. Engler for that support. The comments of two anonymous reviewers were also very helpful.

LITERATURE CITED

ARNAL, R. E., E. DITTMER, AND E. SHUMAKER.
1973. Sand transport studies in Monterey Bay, California. Moss Landing Mar. Lab. Tech. Publ. 73-5, 71 p.

BARNARD, J. L.
1960. The amphipod family Phoxocephalidae in the Eastern Pacific Ocean, with analyses of other species and notes for a revision of the family. Allan Hancock Pac. Exped. 18:175-375.
1963. Relationship of benthic Amphipoda to invertebrate communities of inshore sublittoral sands of Southern California. Pac. Nat. 3:439-467.

BARNARD, J. L., AND F. C. ZIESENHENNE.
1961. Ophiuroid communities of Southern Californian coastal bottoms. Pac. Nat. 2:131-152.

BOUSFIELD, E. L.
1970. Adaptive radiation in sand-burrowing amphipod crustaceans. Chesapeake Sci. 11:143-154.

BRETT, C. E.
1964. A portable hydraulic diver-operated dredge-sieve for sampling subtidal macrofauna. J. Mar. Res. 22:205-209.

CAREY, A. G., JR.
1965. Preliminary studies of animal-sediment interrelationships off the central Oregon coast. *In* Ocean science and ocean engineering 1965, Vol. 1, p. 100-110. Mar. Tech. Soc., Wash., D.C.
1972. Ecological observations on the benthic invertebrates from the central Oregon continental shelf. *In* A. T. Pruter and D. L. Alverson (editors), The Columbia River estuary and adjacent ocean waters, bioenvironmental studies, p. 422-443. Univ. Wash. Press, Seattle.

CLIFTON, H. E., R. E. HUNTER, AND R. L. PHILLIPS.
1971. Depositional structures and processes in the nonbarred high-energy nearshore. J. Sediment. Petrol. 41:651-670.

CODY, M. L.
1974. Competition and the structure of bird communities. Princeton Univ. Press, Princeton, N.J., 318 p.

CONNELL, J. H.
1961. Effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacle *Balanus balanoides*. Ecol. Monogr. 31:61-104.

CONOVER, W. J.
1971. Practical nonparametric statistics. Wiley, N.Y., 462 p.

DAY, J. H.
1967. A monograph on the Polychaeta of Southern Africa: Part 2. Sedentaria. Br. Mus. (Nat. Hist.) Publ. 656, 325 p.

DAY, J. H., J. G. FIELD, AND M. P. MONTGOMERY.
1971. The use of numerical methods to determine the distribution of the benthic fauna across the continental shelf of North Carolina. J. Anim. Ecol. 40:93-125.

DAYTON, P. K.
1971. Competition, disturbance, and community organization: The provision and subsequent utilization of space in a rocky intertidal community. Ecol. Monogr. 41:351-389.

FAGER, E. W.
1968. A sand-bottom epifaunal community of invertebrates in shallow water. Limnol. Oceanogr. 13:448-464.

FIELD, J. G.
1971. A numerical analysis of changes in the soft-bottom fauna along a transect across False Bay, South Africa. J. Exp. Mar. Biol. Ecol. 7:215-253.

FINCHAM, A. A.
1971. Ecology and population studies of some intertidal and sublittoral sand-dwelling amphipods. J. Mar. Biol. Assoc. U.K. 51:471-488.

FOLK, R. L., AND W. C. WARD.
1957. Brazos River Bar: A study in the significance of grain size parameters. J. Sediment. Petrol. 27:3-26.

FORD, R. E.
1965. Distribution, population dynamics and behavior of a bathid fish, *Catharichthys stigmaeus*. Ph.D. Thesis, Univ. California, San Diego, 243 p.

GORDON, B. L.
1974. Monterey Bay area: Natural history and cultural imprints. The Boxwood Press, Pacific Grove, Calif., 202 p.

GRAY, J. S.
1974. Animal-sediment relationships. Oceanogr. Mar. Biol. Annu. Rev. 12:223-262.
HARTMAN, O.
1941. Some contributions to the biology and life history of Spionidae from California. Allan Hancock Pac. Exped. 7:289-322.
HODGSON, A. T., AND J. W. NYBAKKEN.
1973. A quantitative survey of the benthic infauna of northern Monterey Bay, California. Moss Landing Mar. Lab. Tech. Publ. 73-8, 245 p.
HOWARD, J. D., AND H.-E. REINECK.
1972. Georgia coastal region, Sapelo Island, U.S.A.: Sedimentology and biology. IV. Physical and biogenic sedimentary structures of the nearshore shelf. Senckenb. Marit. 4:81-123.
HULBERG, L. W., AND J. S. OLIVER.
1979. Prey availability and the diets of two cooccurring flatfish. *In* C. A. Simenstad and S. J. Lipovsky (editors), Fish food habit studies. Proc. 2d Pac. Northwest Tech. Workshop, October 10-13, 1978. Univ. Wash. Press, Seattle.
KOMAR, P. D.
1976. Beach processes and sedimentation. Prentice-Hall, Inc., 429 p.
KUKOWSKI, G. E.
1973. Results of the Sea Grant fishes sampling program for the 1971-1972 season. Moss Landing Mar. Lab. Tech. Publ. 73-6, 48 p.
LIE, U.
1968. A quantitative study of benthic infauna in Puget Sound, Washington, USA, in 1963-1964. Fiskeridir. Skr. Ser. Havunders. 14:229-556.
1969. Standing crop of benthic infauna in Puget Sound and off the coast of Washington. J. Fish. Res. Board Can. 26:55-62.
LIE, U., AND D. S. KISKER.
1970. Species composition and structure of benthic infauna communities off the coast of Washington. J. Fish. Res. Board Can. 27:2273-2285.
LUBCHENCO, J. L., AND B. A. MENGE.
1978. Community development and persistence in a low rocky intertidal zone. Ecol. Monogr. 48:67-94.
MASSÉ, H.
1972. Quantitative investigations of sand-bottom macrofauna along the Mediterranean north-west coast. Mar. Biol. (Berl.) 15:209-220.
MERRILL, R. J., AND E. D. HOBSON.
1970. Field observations of *Dendraster excentricus*, a sand dollar of western North America. Am. Midl. Nat. 83: 595-624.
MILLS, E. L.
1969. The community concept in marine zoology, with comments on continua and instability in some marine communities: A review. J. Fish. Res. Board Can. 26:1415-1428.
MUUS, K.
1973. Settling, growth and mortality of young bivalves in the Øresund. Ophelia 12:79-116.
NICHOLS, F. H.
1970. Benthic polychaete assemblages and their relationship to the sediment in Port Madison, Washington. Mar. Biol. (Berl.) 6:48-57.
OLIVER, J. S.
1979. Processes affecting the organization of marine soft-bottom communities in Monterey Bay, California and McMurdo Sound, Antarctica. Ph.D. Thesis, Univ. California, San Diego, 310 p.
PAINE, R. T.
1974. Intertidal community structure: Experimental studies on the relationship between a dominant competitor and its principal predator. Oecologia 15:93-120.
REINECK, H. E., AND I. E. SINGH.
1973. Depositional sedimentary environments; with reference to terrigenous clastics. Springer-Verlag, N.Y., 439 p.
RICKETTS, E. F., J. CALVIN, AND J. HEDGPETH.
1968. Between Pacific tides. 4th ed. Stanford Univ. Press, Stanford, Calif., 614 p.
RHOADS, D. C., AND D. K. YOUNG.
1970. The influence of deposit-feeding organisms on sediment stability and community trophic structure. J. Mar. Res. 28:150-178.
RHOADS, D. K.
1974. Organism-sediment relations on the muddy sea floor. Oceanogr. Mar. Biol. Annu. Rev. 12:263-300.
SAMEOTO, D. D.
1969. Some aspects of the ecology and life cycle of three species of subtidal sand-burrowing amphipods (Crustacea:Haustoriidae). J. Fish. Res. Board Can. 26:1321-1345.
SANDERS, H. L.
1958. Benthic studies in Buzzards Bay. I. Animal-sediment relationships. Limnol. Oceanogr. 3:245-258.
1960. Benthic studies in Buzzards Bay. III. The structure of the soft-bottom community. Limnol. Oceanogr. 5:138-153.
SHEPARD, F. P., AND R. F. DILL.
1966. Submarine canyons and other sea valleys. Rand McNally and Co., Chicago, 381 p.
SNEDECOR, G. W., AND W. G. COCHRAN.
1967. Statistical methods. 6th ed. Iowa State Univ. Press, Ames, 593 p.
STEPHENSON, T. A., AND A. STEPHENSON.
1972. Life between tide marks on rocky shores. W. H. Freeman and Co., San Franc., 435 p.
THOMPSON, R. K.
1972. Functional morphology of the hind gut of *Upogebia pugettensis* (Crustacea, Thalassinidae) and its role in burrow construction. Ph.D. Thesis, Univ. California, Berkeley, 240 p.
VANBLARICOM, G. R.
1978. Disturbance, predation, and resource allocation in a high-energy sublittoral sand-bottom ecosystem: Experimental analyses of critical structuring processes for the infaunal community. Ph.D. Thesis, Univ. California, San Diego, 328 p.
WHITTAKER, R. H.
1962. Classification of natural communities. Bot. Rev. 28:1-239.
1967. Gradient analysis of vegetation. Biol. Rev. (Camb.) 42:207-264.

DAILY TIME OF SPAWNING OF 12 FISHES IN THE PECONIC BAYS, NEW YORK

STEVEN P. FERRARO[1]

ABSTRACT

Diel spawning periodicity occurs throughout the spawning season in 11 of 12 fishes studied in the Peconic Bays, New York. The bay anchovy, *Anchoa mitchilli*; Atlantic menhaden, *Brevoortia tyrannus*; northern and striped searobins, *Prionotus carolinus* and *P. evolans*; hogchoker, *Trinectes maculatus*; weakfish, *Cynoscion regalis*; windowpane flounder, *Scophthalmus aquosus*; and butterfish, *Peprilus triacanthus*, spawn primarily in the evening or at night. The tautog, *Tautoga onitis*, and cunner, *Tautogolabrus adspersus*, begin spawning in the afternoon and spawning continues into the night. Scup, *Stenotomus chrysops*, spawns in the morning, and Atlantic mackerel, *Scomber scombrus*, spawns throughout the day.

The prevalence of nocturnal spawners in the Peconic Bays is inconsistent with predictions of hypotheses attributing diel spawning periodicity to reproductive isolation and visual constraints. Some possible causes of diel spawning periodicity are reproductive synchronism between the sexes, deleterious effects of sunlight on embryogenesis, and parent or embryo predator avoidance.

In his review, Woodhead (1966) cited several references indicating that spawning occurs only in the evening or at night in some clupeids, gadids, pleuronectids, exocoetids, and mullets, and only during daylight hours in some gobies, blennies, and pomacentrids. Woodhead concluded: "There is relatively little direct information describing the spawning behaviour of marine fish, but such as is available suggests that spawning is restricted to a particular part of the day." Recent research generally supports that conclusion.

Simpson (1971) determined the time of day of spawning of four marine fishes from the occurrence of recently spawned eggs in plankton collections. His results showed spawning occurs in plaice, *Pleuronectes platessa*, between 1800 and 0700 h; sprat, *Sprattus sprattus*, between 2200 and 0600 h; pilchard, *Sardina pilchardus*, between 2000 and 0200 h; and throughout the day in dab, *Limanda limanda*, but most intensely between 2400 and 1200 h. Wicklund (1970) observed that natural spawning of small (total length <125 mm) cunner, *Tautogolabrus adspersus*, was restricted to between 1200 and 1700 h. A sevenfold difference in numbers of fish eggs in night vs. day plankton collections prompted Hobson and Chess (1978) to suggest that many reef fishes primarily spawn at night. Ten anchovy species in the Gulf of Panama have daily spawning periods lasting about 3 h, and all spawn between about 1700 and 0430 h (Simpson 1959).

Accumulating evidence indicates that diel spawning periodicity is a common phenomenon in marine fishes. In this paper further information is presented on daily spawning times of 12 marine fishes from 10 families.

METHODS

From midspring to late fall 1972, 1973, and 1974 plankton collections were taken usually at 9-13 locations in the Peconic Bay area, Long Island, N.Y. (Figure 1). In 1972 and 1973 samples were taken on two consecutive days at intervals of 5-11 days. In 1974 samples were collected at monthly intervals. All collections were made during daylight hours from 0600 to 1735 h e.s.t. At least three vertical plankton-haul samples were taken from the bottom (or to a maximum depth of 12 m) to the surface at each location with a No. 3 (0.333 mm mesh) conical plankton net with a mouth area of 0.5 m^2. The plankton samples were killed and preserved in 4% seawater Formalin[2] and stored in 1 l glass jars. Surface water temperature and solar time of day (hours since sunrise; time of sunrise

[1]Department of Ecology and Evolution, State University of New York at Stony Brook, Stony Brook, NY 11794.

[2]Reference to trade names does not imply endorsement by the State University of New York at Stony Brook, Stony Brook, N.Y., or the National Marine Fisheries Service, NOAA.

Manuscript accepted October 1979.
FISHERY BULLETIN: VOL. 78, NO. 2, 1980.

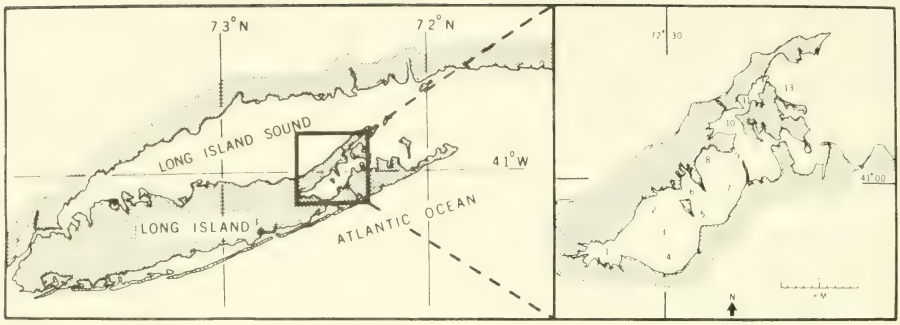


FIGURE 1.—Location of study site and 13 sampling stations in the Peconic Bays, Long Island, N.Y.

from National Ocean Survey 1971, 1972, 1973) of each collection were recorded. Since Peconic Bay waters are well mixed (Hardy 1976), the surface water temperatures were adequate indicators of temperatures of the water column and the natural incubation temperatures of recently spawned fish eggs (see Discussion section).

Over the 3-yr period more than 2,600 samples were collected and processed. Plankton samples were split into manageable subsamples and their entire contents were viewed under a stereomicroscope. Fish eggs were separated, identified to species, staged (Table 1), and counted. Developmental stages in Table 1 are approximately equal in duration when fish embryos are reared at constant temperatures (Ferraro 1980). References used for fish egg identification included: Kuntz (1915), Kuntz and Radcliffe (1917), Hildebrand and Cable (1930, 1934), Merriman and Sclar (1952), Wheatland (1956), Richards (1959), Mansueti and Hardy (1967), Williams (1967), Austin (1973), Berrien (1975), and Colton and Marak[3].

Estimates of time of day of spawning for each species in a sample were determined by estimating the mean age of fish eggs <24 h old using embryo age prediction equations for Atlantic menhaden, *Brevoortia tyrannus*, in Ferraro (1980), below:

$$\log_{10} B = -0.193 + 17.193\,T^{-1} + 34.090\,T^{-2} - 461.276\,T^{-3} \quad (1)$$

[3]Colton, J. B., Jr., and R. R. Marak. 1969. Guide to identifying the common planktonic fish eggs and larvae of Continental Shelf waters, Cape Sable to Block Island. Bur. Commer. Fish. Lab., Woods Hole, Mass., Lab. Ref. No. 69-9, 43 p.

TABLE 1.—Fish embryo stages of development.

Stage	Description
1	Fertilized eggs prior to cell division to 8-cell stage
2	Eight-cell stage to completion of blastodisc formation
3	Blastodisc formation to germ ring ½ way around egg
4	Germ ring ½ way around egg to just prior to blastopore closure
5	Blastopore closure to tail bud beginning to separate from the yolk
6	Tail bud free of yolk to caudal ⅛ of body free of the yolk
7	Caudal ⅛ of body free of yolk to caudal ¼th of body free of yolk
8	Caudal ¼th of body free of yolk to fin fold moderately wide and tail portion of embryo rotated out of embryonic axis and tail approaching head
9	Tip of tail approaching head to hatching

and,

$$A = B\,(S - 1) \quad (2)$$

where B = development time (hours) per stage of development
T = temperature (in degrees Celsius)
S = stage of development (Table 1)
A = mean age (in hours)

and subtracting these values from the time the samples were collected in the field. (Field data on differences in development stages of embryos from consecutive day classes indicated that the *B. tyrannus* embryo age equations introduced little or no error when estimating embryo ages of <24 h of most of the species in this study (see Results).)

RESULTS

Discrete day classes of fish eggs of most species were identified in the field samples. Fish eggs were present in samples at distinct morphological stages of development while other morphological

stages were completely absent. Spring spawners typically had polymodal embryonic stage frequency distributions with one or more embryonic stages absent between adjacent modes. As water in the Peconic Bays warmed, the number of modes in the embryo stage frequency distribution decreased such that by midsummer the distribution was unimodal. Also, as water temperature increased the most recently spawned eggs of most fishes were found at consistently later stages of development.

Indirect evidence from field data indicated that embryonic development rates of most species in this study were similar. Tests of differences between modes of embryo development stages representing two consecutive day classes from field samples at 17° C by a posteriori sums of squares simultaneous testing procedure (Sokal and Rohlf 1969) indicated no significant difference ($P > 0.05$) in embryonic growth per day of *B. tyrannus*; bay anchovy, *Anchoa mitchilli*; tautog, *Tautoga onitis*; *Tautogolabrus adspersus*; and searobins, *Prionotus* spp. Also, age differences between day classes of fish embryos in field samples at temperatures between 15.0° and 17.5° C were calculated using the *B. tyrannus* embryo age prediction Equations (1) and (2). The results (Table 2) showed that the *B. tyrannus* equations gave good predictions of the expected age difference between embryo day classes for most of the species in this study.

With the exceptions of scup, *Stenotomus chrysops*; Atlantic mackerel, *Scomber scombrus*; and to a lesser extent *Tautoga onitis* and *Tautogolabrus adspersus* very few early-cleavage stage eggs were collected in our daytime sampling program.

Mean daily spawning times of fishes were calculated from hourly time of spawning frequency distributions of sample estimates of spawning time (Table 3). The 1974 data were used to compute estimated spawning times of *Stenotomus chrysops*; weakfish, *Cynoscion regalis*; windowpane flounder, *Scophthalmus aquosus*; and butterfish, *Peprilus triacanthus*, and only 1973 data were used to compute the spawning time of the hogchoker, *Trinectes maculatus*. Time of spawning estimates were similar for species where data were available for 2 yr. Histograms of relative frequency distributions of sample estimates of spawning time are presented for 1973 data on *Anchoa mitchilli*; *Brevoortia tyrannus*; *Tautoga onitis*; *Tautogolabrus adspersus*; northern and striped searobins, *Prionotus carolinus* and *P. evolans* (note: the searobins are considered together because their embryos can not be reliably distinguished); and *Trinectes maculatus* in Figure 2. In summary, the results show that *A. mitchilli*, *B. tyrannus*, *P. carolinus*, *P. evolans*, *T. maculatus*, *C. regalis*, *S. aquosus*, and *Peprilus triacanthus* spawn primarily in the evening or at night; *Tautoga onitis* and *Tautogolabrus adspersus* spawn in the afternoon and at night; and *Stenotomus chrysops* spawns in the morning.

There was no evidence of diel spawning periodicity by Atlantic mackerel. Typically, all developmental stages (Table 1) were present in samples containing Atlantic mackerel eggs. The only general trend in the Atlantic mackerel egg data was a decrease in numbers of later developmental stages, presumably due to dispersion or egg mortality.

TABLE 2.—Mean age differences ($\bar{x}$, in hours) of fish embryos representing two consecutive day classes in field samples at temperatures[1] between 15.0° and 17.5° C determined by development stage differences between day classes and embryo age prediction equations for *Brevoortia tyrannus*. The expected age difference is 24 h.

Species	Number of samples	$\bar{x} \pm$ SE
Brevoortia tyrannus	124	25.6 ± 0.40
Anchoa mitchilli	53	21.8 ± 0.31
Stenotomus chrysops	20	20.5 ± 0.48
Cynoscion regalis	15	25.4 ± 1.21
Tautoga onitis	101	24.9 ± 0.43
Tautogolabrus adspersus	53	23.6 ± 0.77
Peprilus triacanthus	4	24.2 ± 1.57
Prionotus spp.	64	22.0 ± 0.39
Scophthalmus aquosus	7	22.0 ± 3.16

[1] Range of temperatures chosen were temperatures at which at least two fish embryo day classes would be present.

TABLE 3.—Mean daily spawning times ($\overline{DST}$, in hours after sunrise) of fishes calculated from hourly frequency distributions of sample estimates of spawning time. Estimated ages of fish eggs <24 h old in field samples were subtracted from their time of collection to obtain sample estimates of spawning time.

Species	Year	N	$\overline{DST} \pm$ SE
Brevoortia tyrannus	1972	198	16.36 ± 0.175
	1973	370	17.84 ± 0.168
Anchoa mitchilli	1972	455	16.09 ± 0.103
	1973	693	16.78 ± 0.078
Stenotomus chrysops	1974	32	5.28 ± 0.276
Cynoscion regalis	1974	74	17.45 ± 0.407
Tautoga onitis	1972	160	15.52 ± 0.200
	1973	447	17.62 ± 0.126
Tautogolabrus adspersus	1972	101	15.40 ± 0.343
	1973	322	15.98 ± 0.215
Peprilus triacanthus	1974	22	18.55 ± 0.881
Prionotus spp.	1972	174	19.19 ± 0.307
	1973	330	19.15 ± 0.197
Scophthalmus aquosus	1974	38	16.68 ± 0.607
Trinectes maculatus	1973	132	16.55 ± 0.110

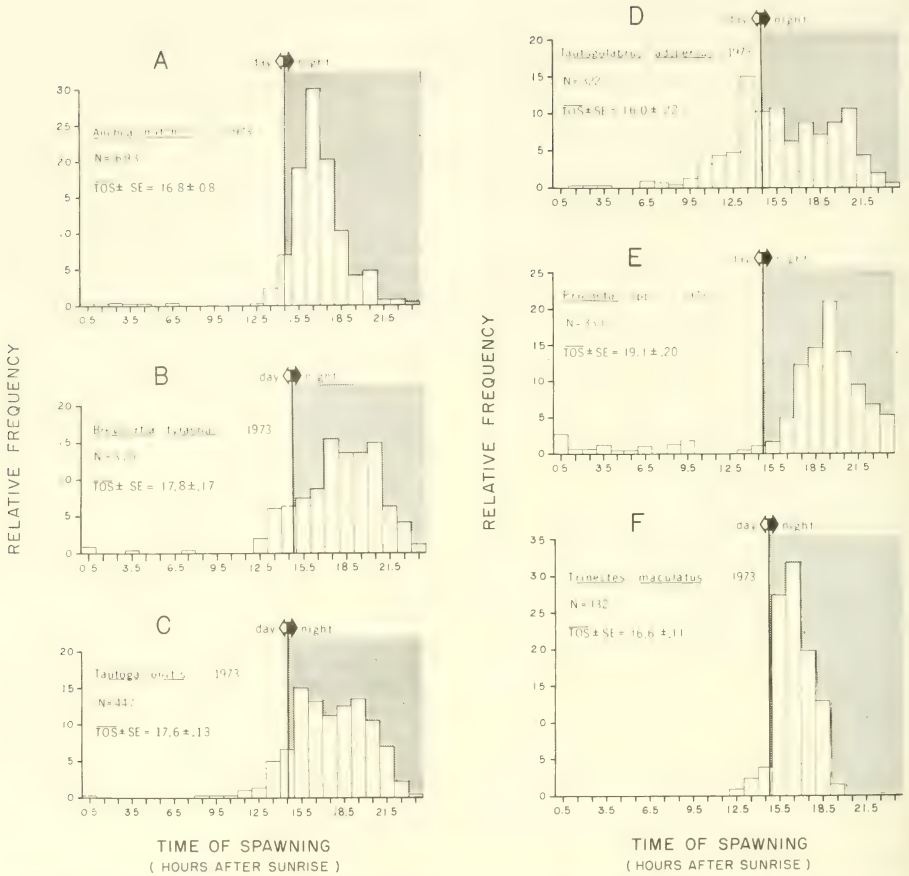


FIGURE 2.—Relative frequency distributions of estimated spawning times (TOS) of (A) *Anchoa mitchilli*, (B) *Brevoortia tyrannus*, (C) *Tautoga onitis*, (D) *Tautogolabrus adspersus*, (E) *Prionotus* spp., and (F) *Trinectes maculatus*, determined by subtracting estimated mean ages of fish eggs + 24 h old from their time of collection in 1973 samples. Mean day length during spawning seasons is indicated.

DISCUSSION

Direct observation of fish spawning at sea is rare, and aquarium observations may not be characteristic of natural spawning or may be difficult or impractical to implement for logistic reasons. Since embryogenesis begins at spawning in most marine teleosts, the time of day spawning occurs can be determined indirectly from the age of embryos captured at sea. Several investigators, including Ahlstrom (1943), Gamulin and Hure (1956), and Simpson (1971), collected plankton samples throughout the day and determined spawning times of fishes from the occurrence of recently spawned eggs. Under certain circumstances (when field temperatures are fairly constant and there is little translocation of eggs) and with knowledge of embryonic development rates, however, spawning times can be back calculated by subtracting age of fish embryos from their time of collection. The method of estimating spawning time of fishes in this paper utilizes field

data commonly obtained in ichthyoplankton research and does not require a continuous field sampling program.

Factors influencing the accuracy of estimated spawning times of fishes in this paper are intraspecific and interspecific differences in development rates of fish embryos and temperature effects on embryo stage (Table 1) duration. Intraspecific differences in development rates are likely to introduce only small and unbiased error in spawning time estimates since incubation times from which age estimates are made are short (<24 h) and mean stages of development of all embryos of a species (<24 h old) in a sample are used in the embryo age calculation. Interspecific differences in development rates of most species in this study are also probably small (see Results). A maximum standard deviation of 2.3 h can be expected in spawning time estimates due to the influence of temperature on embryo stage duration because most fish eggs were collected in water temperatures above 15° C (Ferraro 1980). Surface water temperatures at the time of field collection were probably adequate indicators of natural incubation temperatures of recently spawned eggs since there is little, if any, vertical thermal stratification in the Peconic Bays and surface water temperature at a particular location generally fluctuates by <1° C during a tidal cycle (Hardy 1976).

Based on the occurrence of recently spawned eggs in plankton collections at Beaufort, N.C., Kuntz (1915) and Hildebrand and Cable (1930) concluded that *A. mitchilli* spawned between 1800 and 2100 h (13-16 h after sunrise), and Hildebrand and Cable (1938) concluded that *Trinectes maculatus* spawned between 1800 and 2000 h (13.5-15.5 h after sunrise). Those observations coincide with the onset of spawning estimated for *A. mitchilli* and *T. maculatus* in this paper. Reintjes' (1968) conclusion that *B. tyrannus* spawns at night, Welsh and Breder's (1924) conclusion that *C. regalis* spawns in the evening and at night, and Sette's (1943) calculations showing *Scomber scombrus* spawns throughout the day were confirmed in this research. Wicklund's (1970) observations on the spawning of cunner overlap but have a much shorter duration than that indicated for cunner in Figure 2D. Wicklund (1970) only observed spawning by small (total length <125 mm) cunners between 1200 and 1700 h (7-12 h after sunrise); he never observed larger cunners spawning although they were present and defended territories in his study area. Olla and Samet (1977) noted that tautog in laboratory aquaria spawned almost exclusively between 1330 and 1600 h (7.5-10 h after sunrise). Their experimental fish, however, had been exposed to unnatural photoperiod and temperatures and spawned about 2 mo earlier than tautog normally spawn in nature. Recently spawned eggs in plankton collections indicated that some tautog spawn in the afternoon (8-10 h after sunrise) in the Peconic Bays, but the bulk of tautog spawning appears to take place later in the evening and at night.

A systematic division of fishes in the Peconic Bays and a summary of their spawning times is presented in Table 4. Only Atlantic mackerel showed no indication of diel spawning periodicity, and only scup spawned exclusively during daylight hours. The remaining species spawned primarily during the evening or at night. Nothing exceptional is known about the adult habits or embryos of Atlantic mackerel or scup to suggest why their spawning times are different from the other species. There appears to be no connection between bathymetric distributions of embryos of some of the species (Williams 1968) and spawning time. There was no evidence of constancy in spawning time above the family level. Solar spawning times of most species, though, were consistent throughout the spawning season and in samples collected at different locations, indicating seasonal and local differences in ecologic factors (e.g., temperature, salinity, water depth, tide) had no effect on daily spawning time.

The tendency of marine teleosts with planktonic eggs to spawn in the evening or at night is evident in a listing (Table 5) of some species known or suspected of diel spawning periodicity. There is

TABLE 4.—Systematic division and summary of spawning times (hours after sunrise) of fishes in the Peconic Bays, N.Y. Spawning is indicated by +.

Taxa	Species	Spawning time 0-6	6-12	12-18	18-24
Clupeiformes:					
Clupeidae	*Brevoortia tyrannus*			+	+
Engraulidae	*Anchoa mitchilli*			+	+
Perciformes:					
Sparidae	*Stenotomus chrysops*	+			
Sciaenidae	*Cynoscion regalis*			+	+
Labridae	*Tautoga onitis*		+	+	+
	Tautogolabrus adspersus		+	+	·
Scombridae	*Scomber scombrus*	+	+	+	+
Stromateidae	*Peprilus triacanthus*			+	+
Triglidae	*Prionotus carolinus*			+	+
	Prionotus evolans			+	+
Pleuronectiformes:					
Bothidae	*Scophthalmus aquosus*			+	+
Soleidae	*Trinectes maculatus*			·	

TABLE 5.—Some marine teleosts which spawn planktonic eggs and are known or suspected of spawning only at particular times of the day.

Family and species	Spawning time	Reference
Ophichthidae:		
Pisodonophis cruentifer	Night	Naplin and Obenchain (1980)
Clupeidae:		
Etrumeus teres	Night	Houde (1977)
Sardinella melanosticta	Night	Kamiya (1925)
Sardinops sagax	Evening	Ahlstrom (1943)
Sardinia pilchardus	Evening and night	Gamulin and Hure (1956); Simpson (1971)
Sprattus sprattus	Night	Simpson (1971)
Engraulidae:		
Anchoa hepsetus	Evening and night	Hildebrand and Cable (1930)
A. mitchilli	Evening and night	Kuntz (1915); Hildebrand and Cable (1930)
Cetengraulis mysticetus	Night	Simpson (1959)
Engraulis eurystole	Evening	Kuntz and Radcliffe (1917)
E. mordax	Night	Bolin (1936)
Engraulis spp.	Evening	Delsman (1929)
Stolephorus purpureus	Night	Yamashita (1951)
Stolephorus spp.	Night	Delsman (1931)
Antennariidae:		
Histrio histrio	Afternoon and evening	Walters (pers. commun. in Breder and Rosen 1966)
Gadidae:		
Enchelyopus cimbrius	Morning	Battle (1930)
Gadus morhua	Evening and night	Brawn (1961); Breder and Rosen (1966)
Merluccius merluccius	Morning	Storrow (1913)
Pomatomidae:		
Pomatomus saltatrix	Evening	Norcross et al. (1974)
Carangidae:		
Caranx kurra	Night	Delsman (1926)
C. macrosoma	Night	Delsman (1926)
C. crumenophthalmus	Night	Delsman (1926)
Pomadasyidae:		
Orthopristis chrysoptera	Evening	Hildebrand and Cable (1930)
Sciaenidae:		
Bairdiella chrysura	Evening	Kuntz (1915)
Cynoscion nebulosus	Night	Tabb (1966)
C. regalis	Evening and night	Welsh and Breder (1924)
Labridae:		
Tautoga onitis	Afternoon	Olla and Samet (1977)
Tautogolabrus adspersus	Afternoon	Wicklund (1970)
Scaridae:		
Scarus croicensis	Afternoon	Colin (1978)
Sparisoma rubripinne	Afternoon	Randall and Randall (1963)
Mugilidae:		
Mugil cephalus	Night	Arnold and Thompson (1958)
M. curema	Night	Anderson (1957)
Scombridae:		
Scomber japonicus	Night	Kamiya (1925)
Scomberomorus maculatus	Evening and night	Ryder (1882); Rathbun (1894); Smith (1907)
Pleuronectidae:		
Hippoglossus hippoglossus	Night	Nordgard (1929)
Pleuronectes platessa	Night	Forster (1953); Simpson (1971)
Pelotretis flavilatus	Night	Thomson and Anderton (1921)
Colistium nudipinnis	Night	Thomson and Anderton (1921)
C. guntheri	Night	Thomson and Anderton (1921)
Peltorhamphus novaezeelandiae	Night	Thomson and Anderton (1921)
Rhombosolea plebeia	Night	Thomson and Anderton (1921)
R. tapirina	Night	Thomson and Anderton (1921)
Soleidae:		
Trinectes maculatus	Evening	Hildebrand and Cable (1938)

diel and lunar spawning periodicity in some coral reef fishes (e.g., Lobel 1978; Johannes 1978; May et al.1979). References cited in Breder and Rosen (1966) indicate that at least 70 freshwater and marine teleosts with demersal or attached eggs may spawn or oviposit at particular times of the day. Even though many of the data are only suggestive, there are indications that diel spawning periodicity may be a common and widespread phenomenon among fishes.

Diel spawning periodicity in fishes may be due to physiological constraints or may be adaptive. Woodhead (1966) and Blaxter (1965, 1970) pointed out that light may restrict spawning to a particular time of day, especially in species where vision is important in sexual displays, courtship, and pairing. Woodhead (1966) noted, however, that species which require daylight for courtship might still spawn or oviposit at other times of the day. Obviously, nocturnal spawners are not light limited. If adaptive, the value of reproductive periodicity may be found in the synchronization of reproduc-

tion with the biotic or abiotic environment (Nikolsky 1963; Aschoff 1964; Schwassman 1969). The annual spawning cycle of fishes which may be timed to coincide with the annual production cycle, or a period of low predation, etc. (Nikolsky 1963; Cushing 1969; Hoar 1969), may be the coarse adjustment, and diel spawning time the fine tuning adjustment to temporally changing environmental conditions.

Spawning periodicity may be important in synchronizing reproduction between the sexes (Aschoff 1964; Marshall 1967). The precise daily timing of reproduction may be particularly important in species which engage in mass spawnings. An extreme example are the lancelets (e.g., *Branchiostoma lanceolatum*) which, according to Breder and Rosen (1966), release eggs and sperm into the water at sunset for chance fertilization. Temporally synchronizing spawning in pairing species presumably is more efficient and may optimize the number of receptive encounters.

Marshall (1967) suggested diel spawning periodicity might serve to increase reproductive isolation between related and morphologically similar species. Reproductive isolation may be important in a species-rich habitat such as a coral reef, but many temperate water marine fishes apparently spawn at or about the same time, i.e., in the evening and at night (Tables 4, 5).

Diel spawning periodicity could be an adaptive behavior of fishes to avoid high incident solar radiation during a very sensitive period of embryonic development. Bell and Hoar (1950) and Eisler (1958, 1961) demonstrated the lethal and deleterious effects of light on salmonid embryos, especially during early embryogenesis; and Marinaro and Bernard (1966) demonstrated lethal effects of light, particularly ultraviolet light, on some marine planktonic fish embryos. Perlmutter (1961) and Breder (1962) believed that some characteristics of fish eggs (e.g., transparency, oil droplets, melanophores) were physiological adaptations to minimize deleterious effects of light on fish embryos, and Perlmutter (1961) listed several spawning behaviors of fishes which he thought were adaptions to avoid or minimize exposure of embryos to light. If light is especially harmful to recently fertilized fish eggs, nocturnal spawning could be an adaptive behavior to avoid light during early embryonic development. However, an explanation is then necessary for why light is not a factor for diurnal spawners such as Atlantic mackerel and scup.

Nikolsky (1963) suggested that some fishes spawn at times of day when spawning adults or their eggs will be least susceptible to predation. The "exhausted" condition of some fishes that have recently spawned (Brawn 1961; Breder and Rosen 1966) and evidence of increased vulnerability of some spawning fishes to trawling (Mohr, in Blaxter 1965) tend to support the idea that spawning time may be an adaption to minimize losses due to predation on the parents. Visual predators, predators with diurnal feeding patterns, or predators which undergo diurnal vertical migrations (e.g., ctenophores; Hirota 1974) could subject planktonic fish embryos to different levels of predation over a diurnal cycle. Synchronizing daily spawning time to coincide with a period of low fish embryo predation minimizes fish embryo mortality due to predation. If a fish embryo predator had a diurnal predation cycle of 12 h high and 12 h low predation, Figure 3 shows that a fish spawning at the beginning of a low predation period ensures 50% or more of the embryo incubation time of its progeny will be spent at the low predation level. Qualitatively the results would be the same if changes in predation were gradual and periods of high and low predation were of different durations. Figure 3 also shows that if predation cycles cause diel spawning periodicity, selection for diel spawning periodicity is potentially greater when embryo incubation times are short.

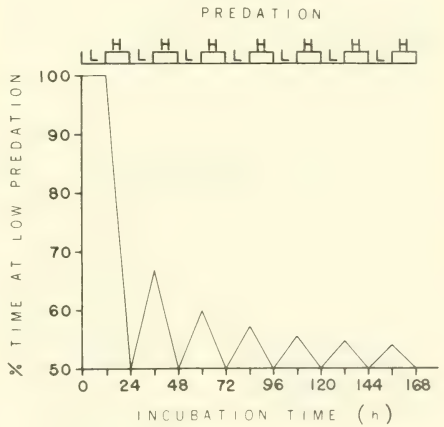


FIGURE 3.—Relationship between percentage of time spent at low predation when spawning occurs at the beginning of a period of low predation and total incubation time of embryos, assuming 12 h alternating periods of low (L) and high (H) predation.

The physiological or adaptive cause(s) of diel spawning periodicity in fishes may become clear as data on its occurrence accumulates or by experiments. Effects of natural maximum solar radiation at the sea surface on different development stages of marine planktonic fish embryos should be studied experimentally. Field studies on fish embryo mortality at different times of day, and studies on feeding patterns of major fish embryo predators and adult fish predators during the spawning season could help elucidate or eliminate some of the factors suspected of causing diel spawning periodicity. If correct, one of the implicit consequences of the diurnal predation cycle hypothesis is that diel spawning periodicity should be more common in fishes with short embryo incubation times (Figure 3), and this prediction should be tested. Additional data on diel spawning periodicity in fishes and studies such as those listed above should ultimately provide important insights into fish physiology, reproductive biology, and ecology.

ACKNOWLEDGMENTS

I thank Kathy Schweyer and William Medeiros for assisting in the laboratory and field work, and Frederick G. Roberts of the Marine Sciences Research Center, State University of New York at Stony Brook, for providing research vessels. I also thank John L. McHugh, Marine Sciences Research Center, State University of New York at Stony Brook, and George Boehlert, Virginia Institute of Marine Science, for reviewing an earlier draft of the manuscript, and *Fishery Bulletin* reviewers for their criticism of the manuscript. Special thanks to George C. Williams, State University of New York at Stony Brook, for reviewing the manuscript and for assistance and support throughout the research.

Research for this paper was financially supported in part by NOAA, Sea Grant Project 2-35281 to G. C. Williams, and by Grant-In-Aid and University Awards from the State University of New York at Stony Brook Research Foundation, and 1977 and 1978 summer Biomedical Research Grants to the author.

LITERATURE CITED

AHLSTROM, E. H.
1943. Studies on the Pacific pilchard or sardine (*Sardinops caerulea*) 4. Influence of temperature on the rate of development of pilchard eggs in nature. U.S. Fish Wildl. Serv., Spec. Sci. Rep. 23, 26 p.

ANDERSON, W. W.
1957. Early development, spawning, growth, and occurrence of the silver mullet (*Mugil curema*) along the South Atlantic coast of the United States. U.S. Fish Wildl. Serv., Fish Bull. 57:397-414.

ARNOLD, E. L., JR., AND J. R. THOMPSON.
1958. Offshore spawning of the striped mullet, *Mugil cephalus*, in the Gulf of Mexico. Copeia 1958:130-132.

ASCHOFF, J.
1964. Survival value of diurnal rhythms. Symp. Zool. Soc. Lond. 13:79-98.

AUSTIN, H. M.
1973. The ecology of Lake Montauk: Planktonic fish eggs and larvae. N.Y. Ocean Sci. Lab., Tech. Rep. 21, 37 p.

BATTLE, H. I.
1930. Spawning periodicity and embryonic death rate of *Enchelyopus cimbrius* (L.) in Passamaquoddy Bay. Contrib. Can. Biol. Fish., New Ser., 5:363-380.

BELL, G. M., AND W. S. HOAR.
1950. Some effects of ultraviolet radiation on sockeye salmon eggs and alevins. Can. J. Res., Sect. D, 28:35-43.

BERRIEN, P. L.
1975. A description of Atlantic mackerel, *Scomber scombrus*, eggs and early larvae. Fish. Bull., U.S. 73:186-192.

BLAXTER, J. H. S.
1965. Effect of change of light intensity on fish. Int. Comm. Northwest Atl. Fish., Spec. Publ. 6:647-661.
1970. 2. Light 2.3 Animals 2.32 Fishes. *In* O. Kinne (editor), Marine ecology, Vol. 1, Part 1, p. 213-320. Wiley-Interscience, Lond.

BOLIN, R. L.
1936. Embryonic and early larval stages of the California anchovy, *Engraulis mordax* Girard. Calif. Fish Game 22:314-321.

BRAWN, V. M.
1961. Reproductive behaviour of the cod (*Gadus callarias* L.). Behaviour 18:177-198.

BREDER, C. M., JR.
1962. On the significance of transparency in osteichthid fish eggs and larvae. Copeia 1962:561-567.

BREDER, C. M., JR. AND D. E. ROSEN.
1966. Modes of reproduction in fishes. Nat. Hist. Press, Garden City, N.Y., 941 p.

COLIN, P. L.
1978. Daily and summer-winter variation in mass spawning of the striped parrotfish, *Scarus croicensis*. Fish Bull., U.S. 76:117-124.

CUSHING, D. H.
1969. The regularity of the spawning season of some fishes. J. Cons. 33:81-92.

DELSMAN, H. C.
1926. Fish eggs and larvae from the Java Sea. 5. *Caranx kurra, macrosoma* and *crumenophthalmus*. Treubia 8:199-211.
1929. Fish eggs and larvae from the Java Sea. 12. The genus *Engraulis*. Treubia 11:275-286.
1931. Fish eggs and larvae from the Java Sea. 17. The genus *Stolephorus*. Treubia 13:217-243.

EISLER, R.
1958. Some effects of artificial light on salmon eggs and larvae. Trans. Am. Fish. Soc. 87:151-162.

1961. Effects of visible radiation on salmonid embryos and larvae. Growth 25:281-346.

FERRARO, S. P.
1980. Embryonic development of Atlantic menhaden, *Brevoortia tyrannus*, and a fish embryo age estimation method. Fish. Bull., U.S. 77:943-949.

FORSTER, G. R.
1953. The spawning behaviour of plaice. J. Mar. Biol. Assoc. U.K. 32:319.

GAMULIN, T., AND J. HURE.
1956. Spawning of the sardine at a definite time of day. Nature (Lond.) 177:193-194.

HARDY, C. D.
1976. A preliminary description of the Peconic Bay estuary. Mar. Sci. Res. Cent., State Univ. N.Y. Stony Brook, Spec. Rep. 3, Ref. 76-4, 65 p.

HILDEBRAND, S. F., AND L. E. CABLE.
1930. Development and life history of fourteen teleostean fishes at Beaufort, N.C. Bull. U.S. Bur. Fish. 46:382-488.
1934. Reproduction and development of whitings or kingfishes, drums, spot, croaker, and weakfishes or sea trouts, family Sciaenidae, of the Atlantic coast of the United States. Bull. U.S. Bur. Fish. 48:41-117.
1938. Further notes on the development and life history of some teleosts at Beaufort, N.C. Bull. U.S. Bur. Fish. 48:505-642.

HIROTA, J.
1974. Quantitative natural history of *Pleurobrachia bachei* in La Jolla Bight. Fish. Bull., U.S. 72:295-335.

HOAR, W. S.
1969. Reproduction. *In* W. S. Hoar and D. J. Randall (editors), Fish physiology, Vol. 3, p. 1-72. Acad. Press, N.Y.

HOBSON, E. S., AND J. R. CHESS.
1978. Trophic relationships among fishes and plankton in the lagoon at Enewetok Atoll, Marshall Islands. Fish. Bull., U.S. 76:133-153.

HOUDE, E. D.
1977. Abundance and potential yield of the round herring, *Etrumeus teres*, and aspects of its early life history in the eastern Gulf of Mexico. Fish. Bull., U.S. 75:61-89.

JOHANNES, R. E.
1978. Reproductive strategies of coastal marine fishes in the tropics. Environ. Biol. Fishes 3:65-84.

KAMIYA, T.
1925. The pelagic eggs and larvae of fishes on the coast of "Hakuriku" (northwestern part of Japan proper). J. Imp. Fish. Inst., Tokyo 21:29-35.

KUNTZ, A.
1915. The embryology and larval development of *Bairdiella chrysura* and *Anchovia mitchilli*. Bull. U.S. Bur. Fish. 33:1-19.

KUNTZ, A., AND L. RADCLIFFE.
1917. Notes on the embryology and larval development of twelve teleostean fishes. Bull. U.S. Bur. Fish. 35:87-134.

LOBEL, P. S.
1978. Diel, lunar, and seasonal periodicity in the reproductive behavior of the pomacanthid fish, *Centropyge potteri*, and some other reef fishes in Hawaii. Pac. Sci. 32:193-207.

MANSUETI, A. J., AND J. D. HARDY, JR.
1967. Development of fishes of the Chesapeake Bay region. An atlas of egg, larval, and juvenile stages. Part I. Nat. Resour. Inst., Univ. Md., College Park, 202 p.

MARINARO, J. Y., AND M. BERNARD.
1966. Contribution à l'etude des oeufs et larves pélagiques de poissons mediterranéens. I. Note preliminaire sur l'influence lethale du rayonnement solaire sur les oeufs. Pelagos 6:49-55.

MARSHALL, J. A.
1967. Effect of artificial photoperiodicity on the time of spawning in *Trichopsis vittatus* and *T. pumilus* (Pisces, Belontiidae). Anim. Behav. 15:510-513.

MAY, R. C., G. S. AKIYAMA, AND M. T. SANTERRE.
1979. Lunar spawning of the threadfin, *Polydactylus sexfilis*, in Hawaii. Fish. Bull., U.S. 76:900-904.

MERRIMAN, D., AND R. C. SCLAR.
1952. The pelagic fish eggs and larvae of Block Island Sound. Bull. Bingham Oceanogr. Collect., Yale Univ. 13:165-219.

NAPLIN, N. A., AND C. L. OBENCHAIN.
1980. A description of eggs and larvae of the snake eel, *Pisodonophis cruentifer* (Ophichthidae). Bull. Mar. Sci. 30: 413-423.

NATIONAL OCEAN SURVEY.
1971. Tide tables, high and low water predictions, 1972: East coast of North and South America, including Greenland. U.S. Dep. Commer., NOAA, Natl. Ocean Surv., Rockville, Md., 290 p.
1972. Tide tables, high and low water predictions, 1973: East coast of North and South America, including Greenland. U.S. Dep. Commer., NOAA, Natl. Ocean Surv., Rockville, Md., 288 p.
1973. Tide tables, high and low water predictions, 1974: East coast of North and South America, including Greenland. U.S. Dep. Commer., NOAA, Natl. Ocean Surv., Rockville, Md., 288 p.

NIKOLSKY, G. V.
1963. The ecology of fishes. (Translated from Russ. by L. Birrett.) Acad. Press, N.Y., 352 p.

NORCROSS, J. J., S. L. RICHARDSON, W. H. MASSMAN, AND E. B. JOSEPH.
1974. Development of young bluefish (*Pomatomus saltatrix*) and distribution of eggs and young in Virginian coastal waters. Trans. Am. Fish. Soc. 103:477-497.

NORDGARD, O.
1929. Notes on fishes I. K. Nor. Vidensk. Selsk. Trondhjem 1:22-23.

OLLA, B. L., AND C. SAMET.
1977. Courtship and spawning behavior of the tautog, *Tautoga onitis* (Pisces: Labridae), under laboratory conditions. Fish. Bull., U.S. 75:585-599.

PERLMUTTER, A.
1961. Possible effect of lethal visible light on year-class fluctuations of aquatic animals. Science (Wash., D.C.) 133:1081-1082.

RANDALL, J. E., AND H. A. RANDALL.
1963. The spawning and early development of the Atlantic parrot fish, *Sparisoma rubripinne*, with notes on other scarid and labrid fishes. Zoologica (N.Y.) 48:46-60.

RATHBUN, R.
1894. Report upon the inquiry respecting food-fishes and the fishing-grounds. Rep. U.S. Fish Fish. Comm. 1892 18:LXXXVIII-CXXXII.

REINTJES, J. W.
1968. Development and oceanic distribution of larval menhaden. *In* Report of the Bureau of Commercial

Fisheries Biological Laboratory, Beaufort, N.C., p. 9-11. U.S. Fish Wildl. Serv., Circ. 287.

RICHARDS, S. W.
1959. Pelagic fish eggs and larvae of Long Island Sound. *In* Oceanography of Long Island Sound, p. 95-124. Bull. Bingham Oceanogr. Collect., Yale Univ. 17(1).

RYDER, J. A.
1882. Development of the Spanish mackerel (*Cybium maculatum*). Bull. U.S. Fish Comm. 1:135-172.

SCHWASSMANN, H. O.
1969. Biological rhythms. *In* W. S. Hoar and D. J. Randall (editors), Fish physiology, Vol. 6, p. 371-428. Acad. Press, N.Y.

SETTE, O. E.
1943. Biology of the Atlantic mackerel (*Scomber scombrus*) of North America. Part I. Early life history including the growth, drift, and mortality of the egg and larval populations. U.S. Fish Wildl. Serv., Fish. Bull. 50:149-237.

SIMPSON, A. C.
1971. Diel spawning behaviour in populations of plaice, dab, sprat, and pilchard. J. Cons. 34:58-64.

SIMPSON, J. G.
1959. Identification of the egg, early life history and spawning areas of the anchoveta, *Cetengraulis mysticetus* (Gunther), in the Gulf of Panama. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm., Bull 3:437-580.

SMITH, H. M.
1907. The fishes of North Carolina. North Carolina Geological and Economic Survey, Vol. II, Raleigh, 453 p.

SOKAL, R. R., AND F. J. ROHLF.
1969. Biometry. The principles and practice of statistics in biological research. W. H. Freeman and Co., San Franc., 776 p.

STORROW, B.
1913. The spawning of the whiting. Rep. Northumb. Sea Fish. Comm., 1913:84.

TABB, D. C.
1966. The estuary as a habitat for spotted seatrout, *Cynoscion nebulosus*. *In* R. F. Smith (chairman), A symposium on estuarine fisheries, p. 59-67. Am. Fish. Soc. Spec. Publ. 3.

THOMSON, G. M., AND T. ANDERTON.
1921. History of the Portobello Marine Fish-Hatchery and Biological Station. N.Z. Board Sci. Art, Bull. 2, 131 p.

WELSH, W. W., AND C. M. BREDER, JR.
1924. Contributions to life histories of Sciaenidae of the eastern United States coast. Bull. U.S. Bur. Fish. 39:141-201.

WHEATLAND, S. B.
1956. Pelagic fish eggs and larvae. *In* Oceanography of Long Island Sound, 1952-1954, p. 234-314. Bull. Bingham Oceanogr. Collect., Yale. Univ. 15.

WICKLUND, R. I.
1970. Observations on the spawning of the cunner in waters of northern New Jersey. Chesapeake Sci. 11:137.

WILLIAMS, G. C.
1967. Identification and seasonal size changes of eggs of the labrid fishes, *Tautogolabrus adspersus* and *Tautoga onitis*, of Long Island Sound. Copeia 1967:452-453.
1968. Bathymetric distribution of planktonic fish eggs in Long Island Sound. Limnol. Oceanogr. 13:382-385.

WOODHEAD, P. M. J.
1966. The behaviour of fish in relation to light in the sea. Oceanogr. Mar. Biol. Annu. Rev. 4:337-403.

YAMASHITA, D. T.
1951. The embryological and larval development of the nehu, an engraulid baitfish of the Hawaiian Islands. M.S. Thesis, Univ. Hawaii, Honolulu, 64 p.

AN IMPROVED METHOD TO ANALYZE TRIMETHYLAMINE IN FISH AND THE INTERFERENCE OF AMMONIA AND DIMETHYLAMINE

FERN A. BULLARD AND JEFF COLLINS[1]

ABSTRACT

The trimethylamine content of most marine fish, especially the gadoid species, is internationally accepted as an index of spoilage. However, ammonia, dimethylamine, and other amines also contribute to the trimethylamine value. Variations in the conditions of the three current methods used to analyze for trimethylamine content were studied in detail to determine the best condition to extract trimethylamine and to reduce the extraction of ammonia, dimethylamine, and other amines. Formaldehyde does not inhibit the interference from ammonia but the interference is negligible even in advanced spoilage. Formaldehyde inhibits the interference from dimethylamine to some extent if KOH is used as the base but increases the interference in the K_2CO_3 method. The extraction of di- and trimethylamine are highly dependent upon the base used and the temperature of extraction. A new method of extracting at −15° C using 45% KOH was developed that essentially eliminates interference from ammonia, dimethylamine, and other amines. To directly compare the methods, the trimethylamine content of a sample of spoiled walleye pollock, *Theragra chalcogramma*, flesh was determined by the three currently used methods and the cold method of extraction. All methods gave similar standard deviations but the K_2CO_3 method gave higher values than the KOH methods and the cold method gave the lowest value. Various levels of trimethylamine and dimethylamine simulating different qualities of fish and frozen storage times were added to samples of Pacific cod, *Gadus macrocephalus*, flesh. The cold method consistently extracts more accurate amounts of trimethylamine with less interference from dimethylamine than any of the other extraction methods.

The trimethylamine (TMA) content of most marine fish, especially the gadoid species, is accepted internationally as an index of spoilage. Dyer's 1959 method of analysis for TMA, except for the concentration of formaldehyde (FA), has been adopted by the Association of Official Analytical Chemists (Horwitz 1975). Trimethylamine is produced by the reduction of trimethylamine oxide by microorganisms (Poller and Linneweh 1926). Ammonia, dimethylamine (DMA), and other volatile bases are also formed when fish spoil and to some extent interfere with the measurement of TMA. In advanced spoilage, some of the higher aliphatic amines are formed by decarboxylation of amino acids and may cause interference (Dyer 1945).

A number of investigators studied the TMA method to improve the accuracy and reduce the effects of ammonia, DMA, and other amines. Dyer (1945) adapted the method of determining amines to fish and used 0.02% picric acid in dry toluene instead of chloroform (Richter 1938; Richter et al. 1941). Dyer and Mounsey (1945) used a trichloroacetic acid (TCA) extract of fresh cod instead of the unstable press juice or weighed samples. Hashimoto and Okaichi (1957) claimed that variation of temperature caused serious errors in the determination of TMA, and recommended a 30° C extraction with 25% KOH rather than 50% K_2CO_3 and room temperature. Tozawa et al. (1971) confirmed these findings and showed that 25% KOH reduced the interference caused by DMA and claimed the formation of a compound from FA and DMA which was not extracted in the presence of hydroxide ions. Murray and Gibson (1972) found that 45% KOH extracted more TMA and gave more linear and reproducible results than if extracted with 25% KOH or 50% K_2CO_3.

The three current methods of analysis for TMA employ 25% KOH, 45% KOH, or 50% K_2CO_3 to release TMA for extraction into the toluene layer and result in different absorbancies for the picrate color with DMA and TMA. In general, the use of K_2CO_3 results in a higher extraction of DMA and a lower extraction of TMA than if KOH were used. Ideally, the best method to measure TMA content should result in complete extraction of TMA and zero extraction of ammonia (NH_3), DMA, and other amines so that these components will not contribute to the TMA value. A new method was

[1]Northwest and Alaska Fisheries Center Kodiak Investigations-Utilization, National Marine Fisheries Service, NOAA, P.O. Box 1638, Kodiak, AK 99615.

Manuscript accepted December 1979.
FISHERY BULLETIN: VOL. 78, NO. 2, 1980.

developed from information obtained from a detailed study of how temperature, type and concentration of base, and the presence (or not) of FA affect the extraction and subsequent absorbancies of the picrate color of NH_3, DMA, and TMA.

EXPERIMENTAL

Purification Procedures

Trimethylamine hydrochloride (TMA·HCl) and dimethylamine hydrochloride (DMA·HCl) were crystallized twice from hot 2-propanol and dried under high vacuum overnight. Reagent grade and previously used toluene was purified by shaking and partitioning with concentrated sulfuric acid in a separatory funnel followed by water, sodium hydroxide, and water; filtering through anhydrous sodium sulfate (NA_2SO_4); and distilling at 110° C. Reagent grade Formalin[2] (37% FA) was shaken with magnesium carbonate, filtered, and diluted 1:9 with water. Hexamethylenetetramine (HMTA) from Pfaltz and Bauer was crystallized twice from hot 2-propanol or from hot, dry toluene and dried overnight under high vacuum. N N N′N′-tetramethylmethanediamine (TMMD) from Pfaltz and Bauer was distilled using a column packed with glass helices. The first 25 ml fraction (72°-81° C) was discarded, the next 25 ml fraction (81° C) was used for analysis, and the final 25 ml distillate was discarded. Reagent grade ammonium chloride (NH_4Cl) was crystallized twice from hot water and dried under high vacuum overnight.

Extraction Procedure for Fish Flesh

Procedures cited in the literature for the extraction of fish have used a specific amount of flesh plus water or TCA followed by shaking or blending and filtration. These methods assume a specific moisture content of the flesh, a total volume, and a complete extraction or uniform dispersion of TMA in the extract, e.g., 100 g flesh at 80% moisture plus 300 ml TCA solution would give a 1/95 aliquot for a 4 ml sample. To improve accuracy of the method, we used an exhaustive extraction-filtration procedure and dilution to a volume. Details of the procedure are given in the Recommended Procedures section.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Methods of Analyses for TMA

Unless otherwise indicated, the three commonly used methods of analyses for TMA were modified slightly to fit our equipment and to reflect recent advances in the methods. The methods of Dyer (1945), Tozawa et al. (1971), and Murray and Gibson (1972) were used as follows: a 4 ml sample of a standard solution in 5% TCA or a 5% TCA extract of fish flesh was added to a 25 × 150 mm screw top test tube, followed by the addition of 10 ml toluene, 1 ml of 3.7% FA solution, and left to stand 5 min before the addition of 3 ml of base (25% KOH, 45% KOH, or 50% K_2CO_3). The tube was tightly sealed using a gasket of a double layer of 1 mil polyethylene film under the cap and shaken for 15 min at room temperature on a Burrell wrist action shaker modified by building-up the platform 20.3 cm with Styrofoam. After standing several minutes, about 7 ml of the toluene layer were removed and dried with 0.5 g anhydrous Na_2SO_4. After drying, 5 ml were added to 5 ml of 0.02% picric acid in dry toluene and the absorbance was determined at 415 nm on a Gilford modified Beckman D.U. spectrophotometer. A fourth method will be referred to as the "cold method" of extraction and uses 45% KOH (Murray and Gibson 1972) but the extraction is done at −15° C. The details of this method are given in the section on Recommended Procedures.

Standard Curves

Since four distinctly different methods were used to analyze for TMA content, complete blank determinations and standard curves were made for each method. The equations for the regression lines (standard curves) of absorbance on concentration of TMA (micrograms TMA-N/milliliter) for each of the methods were as follows:

25% KOH, room temperature	$Y = 0.071X - 0.007$	(1)
45% KOH, room temperature	$Y = 0.087X - 0.001$	(2)
50% K_2CO_3, room temperature	$Y = 0.067X - 0.012$	(3)
45% KOH, cold (−15° C)	$Y = 0.082X - 0.007$	(4)

where Y = absorbance and X = micrograms TMA-N/milliliter.

The trimethylamine values in milligrams TMA-N/100 g flesh were calculated from these equations and from the total volume (250 ml) of 5% TCA extract, weight of extracted fish flesh (75 g), 4 ml of sample extract per tube, and a dilution factor

(K), if present (e.g., for the cold method use Equation (4)):

$$\frac{(A + 0.007)(250 \text{ ml})(100)(K)}{(0.082)(75 \text{ g flesh})(1{,}000\ \mu\text{g/mg})} = \text{milligrams TMA-N/100 g flesh.} \quad (5)$$

RESULTS AND DISCUSSION

In the following sections, the influence of the presence of FA (or not), the type and concentration of base used, and temperature of extraction were determined separately on each component in the reaction and extraction mixture; i.e., 1) NH_3 and HMTA, 2) DMA and TMMD, and 3) TMA. The four methods were directly compared for precision by replicate analyses of a composite sample of minced fish flesh. Finally, accuracy (recovery of TMA and the interference of DMA) was determined for the four methods by direct addition of known quantities of TMA and DMA.

Reaction of Ammonia

Sprung (1940) reported that FA reacts with NH_3 to form HMTA. Under vacuum distillation conditions at 30° C, the addition of FA to solutions of NH_4Cl and Na_2CO_3 rendered the NH_3 nonvolatile but in the absence of FA, NH_3 was volatile (Benoit and Norris 1942). Dyer (1945) claimed that the addition of 1 or 2 ml of 4% FA did not affect the recovery of TMA, and was sufficient to eliminate the interference of NH_3 up to 10-20 times over the usual concentration of trimethylamine nitrogen. Dyer, however, did not directly study the influence of FA on the development of the picric acid color in the presence of NH_3. Researchers studying the TMA method have followed the prior procedures and used FA to tie up NH_3 in the TMA test.

Standard solutions of NH_4Cl in 5% TCA were prepared and used in the three TMA methods. To simulate various stages of spoilage the concentration ranged from 6.6 to 66 μg N/ml; i.e., 2.2-22.0 mg N/100 g flesh. The absorbancies from the NH_4Cl solutions with and without FA (Table 1, columns 1-6) were low and of questionable significance except if 45% KOH was used. The absorbancies seemed to increase with concentration of NH_4Cl and were about the same whether FA were present or not if 50% K_2CO_3 and 25% KOH were used. Even at the higher concentrations, the absorbancies were low and would contribute little to the TMA value. When 45% KOH was used, the absorbancies were much higher than the absorbancies with the other bases and were not affected by FA except at the higher concentrations. Accordingly, FA and NH_3 did not react under these conditions and NH_3 could contribute to the TMA value. To determine if FA would react with NH_3 at elevated temperatures, the same standard solutions in 5% TCA were treated as before but were preheated in the presence of FA at 60° C for 30 min, cooled to room temperature, and 45% KOH added and extracted in the usual way. The absorbancies of the preheated samples were reduced significantly — see columns 5 and 7 in Table 1. The low absorbancies indicated that FA reacted with NH_4Cl when heated and there was no interference through 26.4 μg N/ml sample. The color development in the samples containing 33.0 μg N/ml and more could be caused by: 1) residual NH_3 through an incomplete reaction with FA, 2) NH_3 through a reverse reaction of the product which is assumed to be HMTA, by the law of mass action or chemical equilibrium, and 3) a partial extraction of HMTA by toluene and subsequent reaction with picric acid.

TABLE 1.—Ammonium chloride or hexamethylenetetramine (HMTA): the absorbancies of picrates in the trimethylamine test as affected by the addition of standard solutions of ammonium chloride or hexamethylenetetramine. Samples (columns 1-10) were extracted at room temperature for 15 min (except 9 and 10 which were extracted at −15° C for 60 s by hand), with formaldehyde (+) and without formaldehyde (0).

NH_4Cl or HMTA (μg N/ml)	NH_4Cl 50% K_2CO_3		NH_4Cl 25% KOH		NH_4Cl 45% KOH		NH_4Cl/HMTA 45% KOH		NH_4Cl 45% KOH	
	1 +	2 0	3 +	4 0	5 +	6 0	7[1] +	8 0	9 +	10 0
6.6	0.008	0.000	0.001	0.001	0.008	0.005	0.000	0.012	0.003	0.004
13.2	.012	.000	.001	.005	.024	.015	.000	.012	.013	.006
16.5	.012	.000	.001	.011	.029	.018	.000	.023	.016	.008
26.4	.016	.004	.010	.011	.027	.028	.000	.027	.017	.008
33.0	.004	.008	.000	.014	.042	.049	.023	.032	.019	.016
52.8	.012	.019	.010	.027	.066	.095	.019	.042	.022	.034
66.0	.020	.027	.011	.039	.072	.119	.044	.045	.024	.043

[1]After addition of FA, samples were heated at 60° C for 30 min to allow FA and NH_3 to react. Samples were then cooled, base added, and extracted at room temperature.

To determine if HMTA would react with picric acid, purified HMTA in dry toluene was added to the picric acid reagent. A strong color developed which indicated that HMTA reacted with picric acid. To determine if HMTA would be extracted under the standard conditions of the TMA test using 45% KOH, standard solutions of HMTA were prepared and used in the same manner as NH_4Cl solutions. The absorbancies for the HMTA samples (Table 1, column 8) were similar to the absorbancies of the samples represented by columns 5 and 7 of Table 1. Further, the absorbancies for HMTA samples were not 0 as would be expected from the literature and indicated that either HMTA was extracted by toluene and reacted with picric acid or a partial reverse reaction occurred and NH_3 was extracted and reacted with picric acid. Whether the picrate color was caused by NH_3 or by HMTA, FA did not eliminate the interference of NH_3 when 45% KOH was used. Formaldehyde gave some protection, however, if the reaction mixture was heated at 60° C for 30 min prior to the addition of 45% KOH.

Since NH_3 or HMTA was extracted by toluene at room temperature and reacted with picric acid, NH_3 was extracted at a low temperature to see if the interference could be reduced. The same standard solutions of NH_4Cl were treated as before but were extracted by the cold method. The data given in columns 9 and 10 of Table 1 showed that the absorbancies were at the same general level as the preheated samples and the presence of FA had little effect on absorbance. We conclude that 45% KOH was less effective in releasing NH_3 at −15° C than at room temperature (Table 1, compare columns 5 with 9, 6 with 10) or NH_3 was less extractable by toluene at −15° C. Although other researchers have used FA to eliminate the interference of NH_3, our data showed that FA does not tie up NH_3 under the usual conditions in the analysis for TMA. On practical grounds, the contribution of NH_3 to the TMA value would be quite low because the bases (except 45% KOH) released only a small amount of NH_3 or NH_3 was only slightly extracted by toluene. Even in advanced spoilage such as 22 mg NH_3-N/100 g flesh (66 μg N/ml), the contribution of NH_3 to the TMA value would be equivalent to 0.45 mg TMA-N/100 g flesh if extracted at room temperature with 45% KOH but only 0.10 mg TMA-N/100 g flesh if determined by the cold method.

TABLE 2.—Dimethylamine hydrochloride: the absorbancies of picrates in the trimethylamine test as affected by the three bases used and temperature of extraction. Samples were extracted for 60 s with vigorous hand shaking using 4 ml 15.9 μg DMA-N/ml, with formaldehyde (+) and without formaldehyde (0).

Temperature of extraction (°C)	25% KOH		45% KOH		50% K_2CO_3	
	1	2	3	4	5	6
	+	0	+	0	+	0
−15	0.015	0.067	0.015	0.605	0.119	0.000
0	.016	.130	.031	.657	.200	.000
6	.024	.208	.053	.721	.251	.007
22	.062	.310	.157	.774	.327	.037
30	.079	.371	.361	.967	.453	.088

Reaction of DMA

Several researchers have found that DMA and TMA are not completely extracted by toluene under conditions used in the TMA test unless replicate extractions are made (Castell et al. 1974). Further, different bases resulted in different extractabilities of DMA. Accordingly, we determined the absorbancies of the picrate color using a standard solution of DMA (15.9 μg DMA-N/ml; i.e., 5.3 mg DMA-N/100 g flesh) under various conditions of the TMA test; temperature, base (K_2CO_3 and KOH), replicate extraction, and presence or absence of FA.

A standard solution of DMA·HCl in 5% TCA was extracted with and without FA by the usual methods but the temperature of extraction was varied (−15° C to +30° C) and the tubes were vigorously shaken by hand for 60 s. The extraction of DMA was strongly influenced by the base and by temperature (Table 2). In the absence of FA, the differences in reactivity of the bases in releasing DMA from the hydrochloride salt are shown in columns 2, 4, and 6 (Table 2). At −15° C, 45% KOH released about half of the DMA present, 25% KOH released 1/20th, and K_2CO_3 was unreactive and did not release DMA. The bases were more reactive at higher temperatures than at lower temperatures but had the same order of reactivity. The date also showed that, if released from the salt, DMA was extracted by toluene even at low temperatures. When FA was present however, a different order of release was evident (Table 2, columns 1, 3, and 5) and showed that FA reacted with DMA to give a product having different reactivity with the bases. The order of release (or extractability) for the product was different than for DMA, i.e., high absorbance with K_2CO_3, intermediate with 45% KOH, and low with 25% KOH. Considerable amounts of the product were extracted in the presence of FA at all temperatures in the carbonate system and would result in

a contribution by DMA of 1.69 mg N/100 g flesh to the TMA value at 22° C. In frozen flesh of gadoid fish, the DMA content might be high relative to TMA and would result in a substantial error in the TMA value unless determined at low temperatures with KOH where DMA would contribute 0.1 mg N or less.

We next studied the effects of the three bases and the presence or absence of FA on the total extractability of DMA. Similar extractions were performed by Castell et al. (1974) but these authors only considered the carbonate system with FA present. The same DMA solutions (15.9 μg DMA-N/ml) with or without FA were extracted as before but at room temperature for 15 min, i.e., 4 ml DMA solution, 10 ml toluene, 1 ml FA (or not), and 3 ml base. After removing about 7 ml toluene for drying and reacting with picric acid, the remainder of the toluene layer was carefully aspirated off, 10 ml toluene added, and reextracted. This process was repeated for a total of six extractions. In the absence of FA, DMA was released rapidly from the salt by 45% KOH, about half as fast by 25% KOH, and slowly by 50% K_2CO_3 (Table 3). If FA were present however, many extractions would be required to extract all of the DMA which, in agreement with Sprung (1940), showed that FA reacted with DMA to give TMMD. The data further showed that TMMD was relatively soluble in toluene but the extractabilities were different because each base had a different rate of reaction with TMMD, i.e., a rapid release of TMMD with K_2CO_3 and slow with 25% KOH. The possibility of each base having a different salting-out effect was eliminated when equal absorbancies were obtained if the same extractions were made with the addition of 0.5 g KCl (data not given).

The data also showed that in the carbonate method TMMD was released to the toluene phase more rapidly than DMA and explains the known interference of DMA in the presence of FA by the Dyer (1945) method. Formaldehyde might best be left out in the 50% K_2CO_3 method. The lower picrate color absorbancies in the KOH systems with FA present might also be explained by the law of mass action (equilibrium) as was done in the section on NH_3. In the equilibrium (FA+DMA $\rightleftharpoons$TMMD) the concentrations of FA, DMA, and TMMD in the aqueous phase are dependent on the type and concentration of base. The products (FA and DMA) of the hydrolysis of TMMD would be formed at a rate dependent upon these same variables and DMA would be rapidly removed from the aqueous phase in the KOH systems because of the rapid extraction of DMA by toluene. Since the absorbancies in the KOH systems were relatively low in the presence of FA, the concentration of DMA from the hydrolysis of TMMD must have been low. In the carbonate system however, DMA from TMMD was slowly released from the aqueous phase into the toluene layer. Apparently a low concentration of DMA existed in the equilibrium formed in the carbonate system and favored the extraction of TMMD by toluene. It is likely that both TMMD and DMA were extracted by toluene at rates that depend on the base and temperature used.

To further study the extraction of TMMD, the same multiple extractions described for DMA were made using purified TMMD in 5% TCA but at a slightly lower concentration (15.0 μg TMMD-N/ml). The absorbancies of the TMMD-picrates (Table 4) were nearly the same as the absorbancies of the DMA-picrates (Table 3). The similarity of data between DMA and TMMD inferred again that FA and DMA react to give TMMD. The addition of FA forced the reaction toward TMMD where the type and concentration of base con-

TABLE 3.—Dimethylamine hydrochloride: the absorbancies of picrates in multiple extractions in the trimethylamine test as affected by the three bases used. Samples were extracted for 15 min at room temperature using 4 ml 15.9 μg DMA-N/ml, with formaldehyde (+) and without formaldehyde (0).

Extraction number	25% KOH		45% KOH		50% K_2CO_3	
	1	2	3	4	5	6
	+	0	+	0	+	0
1	0.064	0.416	0.184	1.022	0.498	0.03
2	.042	.175	.160	.204	.273	.02
3	.049	.125	.149	.017	.195	.01
4	.040	.057	.114	.000	114	.02
5	.049	.036	.117	.000	.074	.02
6	.049	.015	.092	000	.051	.02

TABLE 4.—N N N'N'-tetramethylmethanediamine: the absorbancies of picrates in multiple extractions in the trimethylamine test as affected by the three bases used. Samples were extracted for 15 min at room temperature using 4 ml 15.0 μg TMMD-N/ml, with formaldehyde (+) and without formaldehyde (0).

Extraction number	25% KOH		45% KOH		50% K_2CO_3	
	1	2	3	4	5	6
	+	0	+	0	+	0
1	0.051	0.308	0.193	0.882	0.417	0.041
2	.038	.198	.160	.180	.277	.041
3	.046	.123	.142	.028	.185	.044
4	.036	067	.122	.002	.126	.048
5	.039	.031	.090	.000	.081	.028
6	.046	.022	.073	.000	.059	.025

trolled the degree of retention of TMMD in the aqueous phase or its release to the toluene phase. The use of 1 ml 3.7% FA and 4 ml 15.9 μg DMA-N/ml results in a large excess of FA, about 500 times over that required (1 FA to 2 DMA). Consequently, in the absence of added FA where only the stoichiometric amount of FA was present from TMMD, an equilibrium was established in the KOH systems that favored the formation of DMA and its rapid extraction by toluene. A different equilibrium was formed in the K_2CO_3 system that favored the release of TMMD and extraction by toluene.

Extraction of TMA

The extraction of TMA under various conditions of base, temperature, and FA was examined. A standard solution of TMA·HCl in 5% TCA was prepared (15.9 μg TMA-N/ml, i.e., 5.3 mg TMA-N/100 g). This concentration was chosen as it is near the point of unacceptable quality for fish. In the carbonate method (Table 5), the extraction of TMA was highly dependent upon temperature and would result in a lack of precision unless the temperature was controlled as suggested by Hashimoto and Okaichi (1957). Absorbancies were not as dependent upon temperature in the 25% KOH method as with K_2CO_3 and were nearly independent of temperature with 45% KOH. The slightly lower absorbancies with FA present than if not present might be caused by an impurity of DMA or an interference from FA even though FA would not be expected to react with a tertiary amine. As stated in the section on DMA, FA might best be left out in the carbonate method, i.e., only 10% less TMA was extracted than was extracted in the 45% KOH method.

To determine the conditions for maximum extractions of TMA, the same multiple extractions were done as with DMA. In the 45% KOH test (Table 6), 97% of the TMA was removed in the first extraction and the remainder was removed in the second extraction. The first, second, and third extractions removed 80, 17, and 3% with 25% KOH and removed 72, 21, and 6% with 50% K_2CO_3. Standard curves are assumed to compensate for constant experimental errors such as slightly less than 100% extraction of TMA, but the reliability of the data would be questionable with the low recoveries reported here for 25% KOH and 50% K_2CO_3. Neither do standard curves compensate for variable errors such as the observed strong dependence on temperature of the extraction of TMA in the 25% KOH and 50% K_2CO_3 methods (Table 5).

TABLE 5.—Trimethylamine hydrochloride: the absorbancies of picrates in the trimethylamine test as affected by the three bases used and temperature of extraction. Samples were extracted for 60 s with vigorous hand shaking using 4 ml of 15.9 μg TMA-N/ml, with formaldehyde (+) and without formaldehyde (0).

Temperature of extraction (°C)	25% KOH		45% KOH		50% K_2CO_3	
	1 +	2 0	3 +	4 0	5 +	6 0
−17	0.685	0.854	1.312	1.402	0.286	0.682
0	.921	1.099	1.366	1.412	.630	1.027
6	1.050	1.138	1.378	1.391	.722	1.095
21	1.136	1.235	1.373	1.350	1.013	1.218
30	1.198	1.269	1.408	1.420	1.150	1.303

TABLE 6.—Trimethylamine hydrochloride: the absorbancies of picrates in multiple extractions in the trimethylamine test as affected by the three bases used. Samples were extracted for 15 min at room temperature using 4 ml 15.9 μg TMA-N/ml, with formaldehyde (+) and without formaldehyde (0).

Extraction number	25% KOH		45% KOH		50% K_2CO_3	
	1 +	2 0	3 +	4 0	5 +	6 0
1	1.113	1.223	1.384	1.403	0.987	1.245
2	.233	.159	.050	.033	.282	.130
3	.044	.020	.000	.001	.079	.009
4	.003	.005	.000	.000	.016	.003

Comparative Analyses Using Fish Flesh

Walleye pollock, *Theragra chalcogramma*, were held in slush-ice for 9 d and filleted. Twelve separate TCA extractions were made on a composite sample of the ground flesh. Each extract was analyzed in duplicate by each of the three TMA methods and the cold method. Portions of the extracts were neutralized and analyzed for DMA by Dowden's 1938 method, modified slightly by increasing the time of extraction to 15 min on the modified mechanical shaker.

All methods (Table 7) resulted in similar standard deviations but the TMA values were higher in the K_2CO_3 method than in the KOH methods and the cold method of extraction gave the lowest value. The absorbancy data at 22° C of Table 2 can be used to approximate the degree of contribution of DMA to the TMA values in Table 7. The flesh contained 2.25 mg DMA-N/100 g (6.75 μg/ml) and would contribute different amounts to the TMA value according to the method of analysis employed. The data of Table 2 for K_2CO_3 (0.327 *A* at 22° C using 15.9 μg DMA-N/ml) are equivalent

TABLE 7.—Trimethylamine content in mg TMA-N/100 g flesh from 9-d-old walleye pollock using four methods of analysis.

Extract number	Room temperature extraction			−15° C extraction
	25% KOH	45% KOH	50% K_2CO_3	45% KOH
1	9.52	9.84	10.42	9.18
2	9.73	9.76	10.27	9.14
3	9.55	9.78	10.18	9.08
4	9.66	10.01	10.28	8.84
5	9.53	9.92	10.34	8.84
6	9.69	10.07	10.25	9.10
7	9.51	9.93	10.39	9.28
8	9.56	9.78	10.28	8.97
9	9.49	9.82	10.22	9.18
10	9.65	9.79	10.21	8.91
11	9.65	9.75	10.22	9.11
12	9.55	9.82	10.39	9.11
Mean	9.59	9.85	10.29	9.06
SD	.08	.10	.08	.14

to 0.139 A for 6.75 μg DMA-N/ml by a simple ratio, i.e., $0.327A/(15.9\ \mu g$ DMA-N/ml):$X/(6.75\ \mu g$ DMA-N/ml). An equivalent TMA value was calculated to be 0.75 mg TMA-N/100 g flesh from Equations (3) and (5). If corrected for DMA, the TMA value from Table 7 (K_2CO_3) would be 10.29 − 0.75 = 9.54 mg TMA-N/100 g flesh. Similar calculations for the 25 and 45% KOH methods gave corrected values of 9.45 and 9.59 mg TMA-N/100 g flesh. The small contribution of DMA at −15°C (0.015 A) would be 0.05 mg TMA-N/100 g flesh and give a corrected value of 9.01 for the cold method. The TMA values obtained by the three methods of analysis were in good agreement if corrected for DMA. The cold method of extraction gave slightly lower and more accurate values than the other methods. Cold extraction reduced the release and extractability of numerous other interfering substances discussed by Dyer (1945).

Extraction of Fish Flesh with Added TMA and DMA

To determine the recovery of TMA and the interference of DMA, varying amounts of both were added to blended flesh of Pacific cod, *Gadus macrocephalus*, extracted with TCA in the usual way and analyzed for TMA content by four methods. The sample of flesh contained 3.25 mg DMA-N/100 g by Dowden's method (1938). The amount of amine added, the resulting TMA value, and the percentage of the theoretical value (recovery) by each method of analysis are given in Table 8. The TMA values of cod flesh with added TMA (3, 6, 9, and 12 mg) resulted in similar recoveries of TMA by all methods. If 5, 15, 30, and 50 mg DMA were added to the blended flesh, however, the TMA values were unacceptably high by the 50% K_2CO_3, 25% KOH, and 45% KOH methods. The cold method gave acceptable values although the addition of 50 mg DMA-N increased the TMA value from 1.59 to 2.12, i.e., 133% of theory. If the same quantities of DMA were added plus a small amount of TMA (3 mg), only the cold method gave acceptable TMA values. The other methods were strongly influenced by the presence of DMA. However, if larger amounts of TMA were added (12 mg), along with DMA, the influence of DMA was reduced considerably and the 25% KOH and cold methods gave acceptable results.

All methods gave about equal recovery of added TMA provided the DMA content was low. Trimethylamine values by the three published methods were strongly influenced by the relative

TABLE 8.—Trimethylamine values in mg TMA-N/100 g flesh of Pacific cod as affected by different methods of analysis when varying amounts of the TMA·HCl and DMA·HCl salts were added to the flesh before extracting with TCA.

Levels of TMA and DMA added	25% KOH		45% KOH		50% K_2CO_3		Cold method	
	TMA-N (mg)	Recovery (%)	TMA-N (mg)	Recovery (%)	TMA-N (mg)	Recovery (%)	TMA-N (mg)	Recovery (%)
Sample, as is	1.65		1.94		2.36		1.59	
3 mg TMA	4.81	103	5.17	105	4.89	91	4.81	105
6 mg TMA	7.34	96	8.28	104	7.39	88	8.12	107
9 mg TMA	11.62	109	10.71	98	11.39	100	11.32	107
12 mg TMA	13.94	102	15.23	109	17.04	119	14.90	110
5 mg DMA	2.00	121	2.83	146	3.79	161	1.72	108
15 mg DMA	2.47	150	4.24	219	6.32	268	1.77	111
30 mg DMA	3.18	193	5.89	304	10.16	431	1.89	119
50 mg DMA	3.83	232	8.09	417	14.46	613	2.12	133
3 mg TMA + 5 mg DMA	5.21	112	6.14	124	6.84	128	4.60	100
3 mg TMA + 15 mg DMA	5.70	123	7.59	154	9.25	173	4.81	105
3 mg TMA + 30 mg DMA	6.35	137	9.74	197	11.87	221	4.97	108
3 mg TMA + 50 mg DMA	7.78	167	13.10	265	16.35	305	4.98	108
12 mg TMA + 5 mg DMA	14.48	106	16.42	118	19.39	135	15.24	112
12 mg TMA + 15 mg DMA	14.88	109	16.71	120	19.83	138	15.34	113
12 mg TMA + 30 mg DMA	14.93	109	17.90	128	21.17	147	15.16	112
12 mg TMA + 50 mg DMA	15.79	116	19.72	141	24.27	169	15.19	112

amounts of TMA and DMA in the sample. Only the cold method gave TMA values that were nearly independent of the DMA content of all levels of DMA and TMA. If methods other than the cold method are used to analyze for TMA, the history of the fish and sample storage should be known or the DMA content should be determined separately.

RECOMMENDED PROCEDURES

Extraction Procedure for Fish Flesh

Blend a thoroughly mixed composite sample of fish flesh (75 g) with 90 ml of 8.2% (weight/volume) TCA for 5 min at high speed in a Vertis blender. Pour contents of blender jar into a 150 ml medium porosity sintered glass funnel and filter under vacuum. To prevent foaming and plugging of filter, clamp off the suction line after filtering starts and briefly open when required. Reextract residue with 70 ml of 5% TCA for 2 min and filter into the same filter flask and rinse with 5% TCA from a wash bottle. Quantitatively transfer the combined filtrates and washings to a 250 ml volumetric flask and dilute to the mark with 5% TCA. The extract (4 ml) is used in the TMA analysis without dilution but, if required, 4 ml of a diluted extract is used rather than smaller volumes of extract.

Cold Method of Analysis for TMA

Add 4 ml samples of standard solutions of TMA·HCl in 5% TCA or 5% TCA extracts, 10 ml toluene, and 1 ml of 3.7% FA to 25 × 150 mm screw top test tubes. Allow to stand for 5 min then place tubes in an ice-water bath in an effort to avoid the possible yellow color caused by the addition of concentrated KOH (Castell et al. 1974). When completely chilled, add 3 ml 45% KOH and tightly seal tubes, invert twice, and place in a mixture of salt and precooled saturated brine-ice at −15° C. Use a pump or stirring motor to maintain constant temperature by circulating the brine through the salt, brine-ice mixture. After 2 min, remove the test tubes and shake vigorously by hand for 15 s and replace in the cold bath for 2 min. Repeat this procedure three times for a total of 60 s of vigorous hand shaking. After settling (almost immediately), transfer about 7 ml of the toluene layer to clean dry 18 × 150 mm test tubes and dry with about 0.5 g anhydrous Na_2SO_4 by swirling (Vortex Mixer). After drying, remove 5 ml and add to 5 ml of 0.02% picric acid in dry toluene. Determine the absorbance at 415 nm using 1 cm standard silica cells and a Gilford modified Beckman D.U. spectrophotometer. Determine the blank in the same manner but use 4 ml TCA. Calculate the TMA content in mg TMA-N/100 g from the absorbance and Equations (4) and (5).

SUMMARY

Although NH_3, DMA, and other amines contribute to the TMA value, the TMA content of some marine fish, especially gadoid species, is accepted internationally as an index of spoilage. Variations in the conditions of the three methods used to analyze for TMA were studied to determine the best condition to extract TMA and to reduce the extraction of HN_3, DMA, and other amines. We found that NH_3 was not tied up by FA as suggested in the literature but has little affect on the TMA value of fish even in advanced spoilage. The amount of DMA extracted was strongly dependent on the temperature of extraction, the base used, and the presence or absence of FA. Formaldehyde and DMA reacted to form a compound that was rapidly extracted by 50% K_2CO_3 and very slowly by 25% KOH. If DMA and TMMD were extracted, the absorbancies were nearly the same which infers that the compound formed from FA and DMA was TMMD. The amount of TMA extracted was strongly dependent on the temperature of extraction when 25% KOH or 50% K_2CO_3 was used as the base but nearly independent when 45% KOH was used. A cold method of extraction (45% KOH and −15° C) was developed that essentially eliminated the contribution of DMA to the TMA value. Trimethylamine was determined in spoiled fish flesh by the cold method and the three other methods. Standard deviations were similar for all four methods. The K_2CO_3 method gave the highest value and the cold method gave the lowest value. If varying amounts of TMA and DMA were added to Pacific cod flesh and analyzed by the three published TMA methods, the recovery of TMA and interference from DMA was strongly influenced by the relative amounts of TMA and DMA present. Relative to the other methods, the cold method gave TMA values that were independent of the presence of DMA or the relative amounts of DMA and TMA. We recommend that the cold method be used because it extracts most of the TMA (97%), gives good recovery of added

TMA, is nearly independent of DMA content, and is not affected by other amines or NH_3.

LITERATURE CITED

BENOIT, G. J., JR., AND E. R. NORRIS.
1942. Effect of formaldehyde on the volatilizations of ammonia, mono-, di-, and trimethylamines. Ind. Eng. Chem., Anal. Ed. 14:823-825.

CASTELL, C. H., B. SMITH, AND W. J. DYER.
1974. Simultaneous measurements of trimethylamine and dimethylamine in fish, and their use for estimating quality of frozen-stored gadoid fillets. J. Fish. Res. Board Can. 31:383-389.

DOWDEN, H. C.
1938. The determination of small amounts of dimethylamine in biological fluids. Biochem. J. 32:455-459.

DYER, W. J.
1945. Amines in fish muscle I. Colorimetric determination of trimethylamine as the picrate salt. J. Fish. Res. Board Can. 6:351-358.
1959. Report on trimethylamine in fish. J. Assoc. Off. Agric. Chem. 42:292-294.

DYER, W. J., AND Y. A. MOUNSEY.
1945. Amines in fish muscle II. Development of trimethylamine and other amines. J. Fish. Res. Board Can. 6:359-367.

HASHIMOTO, Y., AND T. OKAICHI.
1957. On the determination of trimethylamine and trimethylamine oxide. A modification of the Dyer method. Bull. Jpn. Soc. Sci. Fish. 23:269-272.

HORWITZ, W. (editor).
1975. Official methods of analysis of the Association of Official Analytical Chemists. 12th ed. Assoc. Off. Anal. Chem., Wash., D.C., 1094 p.

MURRAY, C. K., AND D. M. GIBSON.
1972. An investigation of the method of determining trimethylamine in fish muscle extracts by the formation of its picrate salt-Part I. J. Food Technol. 7:35-46.

POLLER, K., AND W. LINNEWEH.
1926. Uber das Vorkommen von Trimethylamin-oxyd in Clupea harengus. (The occurrence of trimethylamine oxide in *Clupea harengus*.) Ber. Dtsch. Chem. Ges. 59:1362-1365.

RICHTER, D.
1938. Elimination of amines in man. Biochem. J. 32:1763-1769.

RICHTER, D., M. H. LEE, AND D. HILL.
1941. The rate of removal of amines from the blood. Biochem. J. 35:1225-1230.

SPRUNG, M. M.
1940. A summary of the reactions of aldehydes with amines. Chem. Rev. 26:297-338.

TOZAWA, H., K. ENOKIHARA, AND K. AMANO.
1971. Proposed modification of Dyer's method for trimethylamine determination in cod fish. *In* Rudolf Kreuzer (editor), Fish inspection and quality control, p. 187-190.

PERCENTAGE OF STARVING NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, LARVAE IN THE SEA AS ESTIMATED BY HISTOLOGICAL METHODS

CHARLES P. O'CONNELL[1]

ABSTRACT

The proportion of starving larvae of northern anchovy, *Engraulis mordax*, was estimated for the Southern California Bight in March 1977 from histological examination of larvae for 64 1 m net tow samples. The number of larvae in the tows varied from 0 to about 400. Approximately 6 per tow were sectioned and examined with the light microscope. Twenty-six specimens were identified as emaciated from anomalies of the trunk musculature and digestive tract. Some of the emaciated larvae occurred as isolated cases at widely scattered locations, but most were from a few nearshore tows, indicating "patches" of starving larvae. Temperature and plankton volume data indicate that the patches were associated with fluctuating environmental conditions. The samples indicate that about 8% of northern anchovy larvae in the Southern California Bight were starving.

One of the goals in investigations of pelagic fish stocks is that of predicting how large year classes will be at the time they are recruited to the fishery. One of the primary approaches to this problem has been the estimation of larval mortality rates based on abundance estimates from egg and larval surveys. While such surveys will probably continue to be the most reliable source of information on abundance at early ages, the high costs and time delays in processing samples are reasons for seeking alternative approaches (Hunter 1976b). Recently, Lasker (1975, in press) has developed a promising index based on availability of food in concentrations suitable for survival of early feeding stages of the northern anchovy, *Engraulis mordax*.

This study reports another approach that could provide an independent prediction of year class strength for the northern anchovy; namely, estimation by histological methods of the proportion of larvae in the sea showing symptoms of starvation. Since level of mortality in a population is likely to be some function of the proportion of larvae observed to be starving, the proportion, if based on adequate sampling, could be an indicator of ultimate year class success.

Condition factor (Blaxter 1971), chemical indices (Ehrlich 1974), morphometric analyses (Shelbourne 1957; Nakai et al. 1969; Ehrlich et al. 1976; Theilacker 1978), and histological analyses (Umeda and Ochiai 1975; O'Connell 1976; Theilacker 1978) have all been used with some success to characterize the starving condition in larvae of various marine species, in most cases under controlled laboratory conditions. The histological approach differs from the others in that the criteria of starvation are based on qualitative changes in the character of cells and tissues, not on quantitative measurements. Histological criteria developed earlier for northern anchovy larvae starved in the laboratory (O'Connell 1976) were the principal guidelines for evaluating the condition of ocean-caught larvae in this study.

METHODS

In March 1977, 64 net tows were taken over a 12-d period from the NOAA ship *David Starr Jordan* to obtain northern anchovy larvae for histological study. Almost half of the tows were taken between 2 and 10 mi (3.7-18.5 km) from the coast, most were near Newport Beach, Calif., where northern anchovy eggs and larvae were abundant, but some were much farther offshore. A surface temperature was taken by bucket thermometer at each net tow station.

Net tows were taken with a 1 m plankton net on which the cod end was a cylindrical Plexiglas[2]

[1]Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Manuscript accepted October 1979.
FISHERY BULLETIN: VOL. 78, NO. 2, 1980.

bucket (length 30.5 cm, diameter 10 cm) that could be removed quickly. Tows were of short duration to minimize the time larvae would be under stress during capture. The net was let out at a fast steady rate to a depth of 20 m, and then retrieved at a moderate rate. The mean tow time was 3 min (SD = 40 s).

The net drained rapidly as it was hauled out of the water, leaving the cod end cylinder filled with water containing a light to moderate amount of plankton. The contents of the cylinder were immediately poured into a small sieve made of 0.505 Nitex mesh netting, and the sieve was then suspended in Bouin's fluid to fix the concentrated plankton. The total elapsed time from start of tow, when the plankton net first entered the sea surface, to submergence in Bouin's averaged 5 min, 8 s (SD = 1 min, 9 s). After the initial fixation, about 10 or 15 min, the sample was transferred from the sieve to a jar of fresh Bouin's, and this was replaced by 70% ethyl alcohol 2 or 3 d later.

In carrying out the above procedure the inside of the plankton net was not washed down after retrieval until the cod end containing the sample had been removed. After the cod end was removed, the inside of the net was hosed down thoroughly in preparation for the next tow.

Subsequent to the cruise, all northern anchovy and other fish larvae were sorted out of the samples and counted. From those tows containing only a few northern anchovy larvae, all were set aside for sectioning. From those tows containing many larvae, about half a dozen were chosen for sectioning. The number was approximately doubled for a few samples of special interest, e.g., offshore banks. Specimens were picked at random by putting all northern anchovy larvae from a given tow in a shallow, wide-mouth container and repeatedly dipping with a vial as the contents were swirling slowly. During this procedure small specimens with obvious yolk sacs were rejected because they represented nonfeeding larvae not yet vulnerable to starvation.

The total number of larvae selected for sectioning was 318. Standard length was measured with an ocular micrometer, then each specimen was imbedded in paraffin, sectioned serially as close to the sagittal plane as feasible, and stained in Harris' hematoxylin and eosin-phloxine B. Prior to microscope examination the mounted specimens were put in random order with their identities concealed.

Histological criteria similar to those diagnostic for laboratory starved larvae were readily established for ocean-caught larvae by preliminary examination of a few dozen (unidentified) specimens, after which all ocean-caught larvae were classified as to condition. Under Results, the histological indications of condition are described first, and then the classification of larvae is examined in relation to other variables, i.e., standard length, geographical distribution, temperature, and plankton volume.

RESULTS

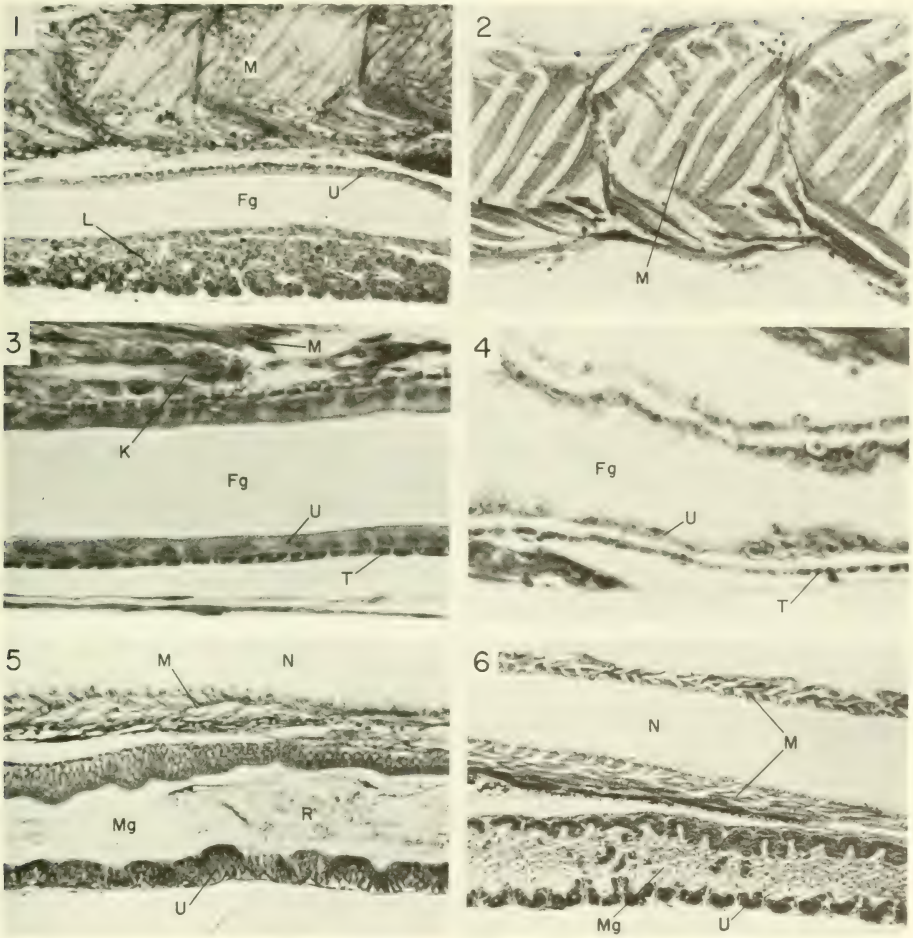
Histological Characteristics of Condition

O'Connell (1976) found the most noticeable effects of artificial starvation of northern anchovy larvae just beyond yolk absorption (3-5 mm) to be cellular dissociation with loss of zymogen in the pancreas, separation and hyalinization of trunk muscle fibers, and shrinkage of the notochord. In the ocean-caught material examined in the present study, specimens ranging from 2.5 to 10 mm showed anomalies in the trunk musculature and notochord, and occasionally also in the pancreas, that closely resembled the effects of starvation in the laboratory material. These larvae almost always showed, in addition, certain irregularities in the histology of the foregut and the midgut that were more striking than effects seen in the digestive tracts of artificially starved larvae.

Trunk Musculature

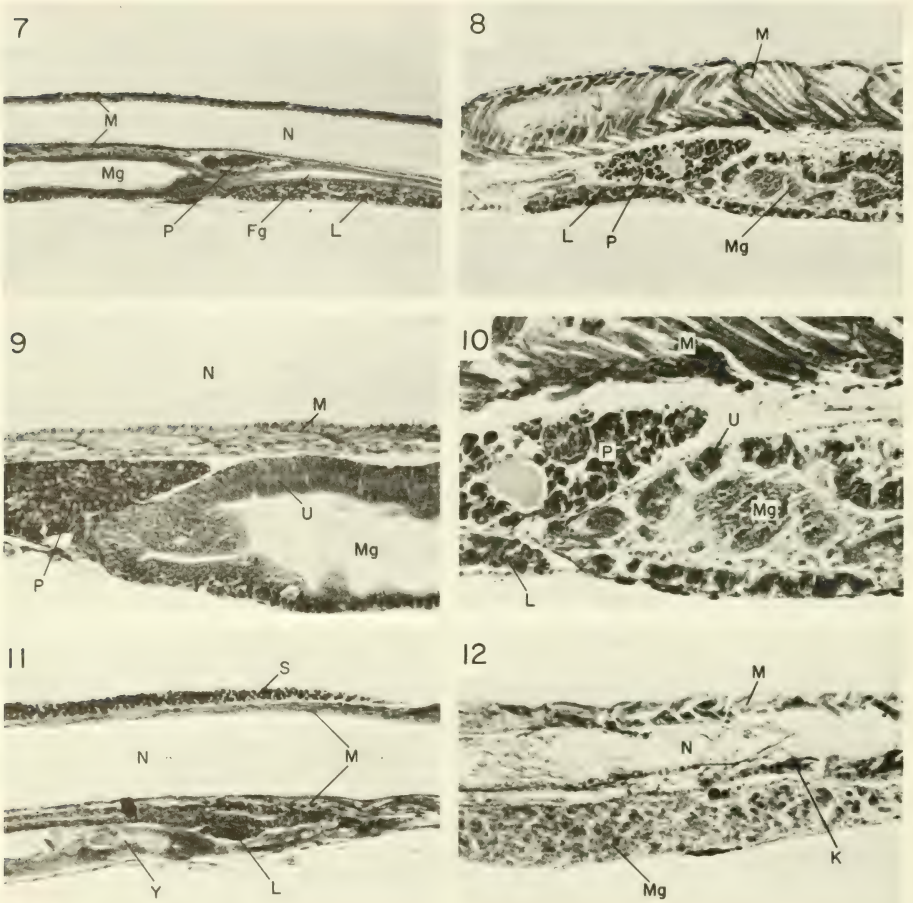
The trunk musculature in the majority of larvae showed good integrity and texture, forming a compact, solid sheet over the lateral surfaces of the notochord, with evident intermuscular matrix tissue and only occasional small separations (Figure 1). The notochord in such larvae generally had a smooth profile and was rarely separated from the musculature. In some specimens, however, the muscle fibers were noticeably separated from each other throughout, indicating an anomalous condition. In the more extreme cases (Figure 2) the fibers were widely separated with degraded fibril clarity, and matrix tissue was greatly reduced. In such specimens the notochord was also irregular in profile, imparting a "lumpy" shape to the trunk of the animal as a whole.

Degraded musculature, of course, might be the result of some process other than starvation. One possibility is capture myopathy, which has been



FIGURES 1-6.—Histological comparisons of healthy (left) and emaciated (right) northern anchovy larvae. All sections are approximately sagittal. 1) The trunk musculature, cut tangential to the body surface, forms a solid sheet. The foregut mucosa is composed of uniform cuboidal cells. 6.1 mm SL; 250×. 2) The trunk musculature, cut tangentially, shows widely separated fibers. 8.5 mm SL; 250×. 3) The foregut mucosa is composed of uniform thick cuboidal cells. 7.0 mm SL; 630×. 4) The foregut is irregular and the cells of the mucosa are diminished in size. 6.1 mm SL; 630×. 5) The mucosa of the midgut shows good integrity and organization, and the lumen contains moderate food residue. 6.3 mm SL; 250×. 6) The midgut is filled with disassociated cellular debris and the mucosa is fragmentary. Separated trunk muscle fibers are also visible. 8.5 mm SL; 250×. Symbols: Fg, foregut; K, kidney; L, liver; M, trunk muscle; Mg, midgut; N, notochord; R, food residue; T, transverse muscle coat of digestive tract; U, mucosa.

reported for a number of ungulates, primates, and birds (Harthoorn 1977) and in the swordfish, *Xiphias gladius* (Tibbo et al. 1961). The outstanding symptom is degeneration of skeletal muscle, presumably from acidemia from overexertion during intense flight and struggle in capture. Though the possibility cannot be entirely dismissed, capture myopathy seems an unlikely cause of the



FIGURES 7-12.—Histological comparisons of healthy (left) and emaciated (right) northern anchovy larvae.—Continued. 7) The trunk muscles cut in cross section above and below the notochord are compact. The foregut and midgut have mucosa of good thickness and integrity. 5.5 mm SL; 100×. 8) Trunk muscles are separated and uneven, the midgut is filled with disassociated cellular material, and the pancreas is severely disassociated. 5.5 mm SL; 100×. 9) Portions of the midgut, the pancreas, and the trunk musculature below the notochord all show good integrity. 5.0 mm SL; 250×. 10) Enlargement of Figure 8 for comparison of pancreas to that in Figure 9. 250×. 11) The foregut is regular and the trunk muscles are compact. The foregut is not yet expanded, and the midgut is not visible in the section. The remnant of the yolk sac, primarily periblast tissue, is prominent. 2.5 mm SL; 250×. 12) The midgut is a solid mass of necrotic debris. The notochord and trunk muscles are collapsed and irregular. The kidney is necrotic. 2.2 mm SL; 250×. Symbols: Fg, foregut; K, kidney; L, liver; M, trunk muscle; Mg, midgut; N, notochord; P, pancreas; S, spinal cord; U, mucosa; Y, yolk.

muscle deterioration observed in the northern anchovy larva. It is essentially a phenomenon of protracted struggle in large animals. In the case of the northern anchovy larvae, time and physical manipulation were minimized in capture.

Depletion of tissues arising from starvation

seems a more likely cause of muscle deterioration. Love (1974), in summarizing depletion in (adult) fishes, states that ". . . when fish are starved the lipid reserves . . . decrease to a certain point beyond which the muscle protein is mobilized. As the protein decreases, the water increases, and this change is mainly brought about by shrinkage of the cells and a corresponding increase in the fluid between them." In conjunction with these findings it had been shown that extracellular spaces appeared in the musculature of Atlantic cod, *Gadus morhua* (Love et al. 1968), and American plaice, *Hippoglossoides platessoides* (Templeman and Andrews 1956). Deterioration of the musculature was a prominent effect following artificial starvation of early postyolk-sac northern anchovy larvae (O'Connell 1976) and of jack mackerel, *Trachurus symmetricus*, larvae (Theilacker 1978). Deterioration of musculature during starvation has also been observed in larval herring, *Clupea harengus*, and plaice, *Pleuronectes platessa* (Ehrlich et al. 1976).

Digestive Tract

In most larvae the long foregut was straight with a uniform lumen and a smooth surfaced mucosa of cuboidal or thick squamous cells (Figure 3; see also Figures 1 and 7). The foregut was considered anomalous if the profile was noticeably irregular in sagittal view. The mucosa usually also showed some variation in cell thickness and shape. In the more extreme cases the mucosa cells tended to be reduced to little more than the nucleus (Figure 4), and the lumen sometimes contained a few sloughed cells.

The midgut varied greatly in appearance, depending on the degree of longitudinal folding and transverse ridge development and on the plane of a particular section. Nevertheless, in most specimens a substantial lumen, sometimes containing food, and a simple mucosa of low columnar cells could be traced (Figures 5, 7, 9). Although the infranuclear portions of the cells were often narrowed and slightly separated, the supranuclear portions were always well joined.

The midgut was judged anomalous when little or no lumen could be traced, or when the traceable lumen contained a considerable bulk of loose nuclei and necrotic cellular debris, and the mucosa proper was fragmenting (Figures 6, 8, 10). In the worst case the midgut was a homogeneous mass of necrotic debris enclosed in only a basement membrane, with no trace of either lumen or mucosa (Figure 12). This specimen, which happened to be the smallest examined, also showed a severely collapsed notochord and degenerate musculature. The degree of organ development, including fully pigmented eyes, indicated that it had shrunken. Healthy specimens of comparable size, which still had unpigmented eyes, showed good notochord and musculature, and often a sizable remnant of the yolk sac (Figure 11). Shrinkage has been shown in laboratory starved larvae of both the Atlantic herring (Blaxter and Hempel 1963) and the northern anchovy (O'Connell 1976; O'Connell and Raymond 1970).

Whereas the muscle and foregut anomalies are at least logically acceptable as consequences of inadequate nourishment, interpretation of the midgut anomaly is problematical. In artificially starved northern anchovy larvae the midgut showed thinning and increased separation of cells, and the loss of some cells (O'Connell 1976), but not strong contraction followed by general fragmentation and necrosis of the mucosa as seen in some of the ocean-caught specimens. It may be, of course, that the symptoms were different because the laboratory and ocean situations were different. Laboratory animals were starved without ever having an opportunity to feed, whereas the oceanic larvae showing symptoms undoubtedly did have the opportunity to feed. Most in fact had processed food through the digestive tract, as indicated by the presence of supranuclear inclusion bodies in the mucosa cells of the hindgut, though the hindgut and the inclusion bodies were sometimes in a state of disintegration. Such inclusion bodies were never found in laboratory specimens deprived of food from time of hatching (O'Connell 1976).

Contraction and congestion resembling that seen in the midguts of the emaciated northern anchovy larvae from the ocean have been described for some other fishes, but they can be symptomatic of disease as well as of starvation. *Clupea harengus* larvae of 9-13 mm, for example, are vulnerable to a nematode that grows in the body cavity and deforms the gut, often resulting in occlusion of the lumen that blocks food intake and/or defecation (Margolis 1970). There are other nematodes whose larvae attack the gut walls of certain fishes, causing inflammatory and degenerative changes, including localized necrosis and infiltration of abundant lymphocytes (Margolis 1970). There are also protozoans, such as

Nosema anomala, which invade the intestinal wall of the young of the threespine stickleback, *Gasterosteus aculeatus*, and generate hypertrophied cells filled with its vegetative and reproductive stages (Lom 1970). Certain viral diseases produce degenerative changes that include necrosis and sloughing of intestinal epithelium (Yasutake 1975). On the other hand, starvation of immature salmon cause, among other things, marked atrophy of the stomach with degeneration of the epithelium, which ". . . could presumably be used for nourishment" (Love 1974). Starvation of

TABLE 1.—Numbers of northern anchovy larvae and other data by net tow for March 1977, off southern California. Number emaciated and standard length pertain only to sectioned larvae. See Figures 13 and 14 for tow locations.

Tow	Date	Hour	Temperature (°C)	Plankton volume (ml)	Number of Larvae		Mean standard length	Number emaciated		
					In tow	Sectioned		Severe	Moderate	Incipient
1	17	1530	13.2	1	0					
2		1750	13.8	5	9	6	4.6			
3		2210	13.5	4	33	7	4.0	1		
4	18	0825	14.2	2	9	5	5.0			
5		1035	14.5	2	9	5	4.9			
6		1440	14.7	3	14	6	6.4			
7		1910	14.7	3	68	6	5.4			
8		2340	14.8	2	47	6	4.7			
9	19	0350	13.7	3	54	6	4.5	3	1	
10		1010	15.2	4	7	7	4.9	3		1
11		1215	15.6	3	2	2	3.9		1	
12		1550	15.5	1	32	6	5.1			
[1]13		1600		8	[2]200	6	5.2			2
14		2215	14.6	11	43	6	4.7			
15	20	0005	13.4	4	24	10	6.7	4	1	2
16		0735	13.6	4	59	6	4.7			
17		1155	14.0	10	20	7	5.5			
[1]18		1205		3	15	6	4.2			
19		2045	15.0	7	70	6	5.5			
20	21	0005	14.9	4	65	7	6.5	4	2	1
21		2045	14.2	21	[2]400	6	5.0			1
22	22	1920	14.2	7	16	6	5.7			
23		2255	13.6	32	[2]350	7	6.0			
24	23	0945	14.6	6	40	6	4.2			
[1]25		0955		10	54	6	4.4			
26		1110	14.7	3	5	5	4.4			
27		2045	14.1	12	180	6	4.9			
28		2315	13.4	7	56	5	5.4		1	
29	24	1020	14.7	14	62	6	5.3			
[1]30		1030		8	67	7	5.3			
31		1440	13.7	7	8	6	5.4			1
32		1915	14.8	11	[2]200	6	4.7			1
33	25	0120	13.8	35	[2]300	6	4.9			
34		1550	13.1	14	97	7	4.8			
[1]35		1555		5	22	6	5.7			
36		2310	13.4	6	122	7	6.9			
37	26	0140	13.1	38	[2]250	6	7.1			
38		0345	12.7	10	19	6	6.6			
39		0550	12.3	33	4	4	12.5			
40		0730	12.8	17	0					
[1]41		0740		29	0					
42		0927	12.7	106	1	1	8.0			
43		1300	14.4	4	1	1	5.9			
[1]44		1325		21	1	1	12.2			
45		1620	14.1	1	0					
[1]46		1630		12	1	1	8.5			
47		1745	14.5	7	0					
48		2030	14.2	13	2	2	10.6			
49		2205	14.2	21	2	2	9.3			
50		2345	14.3	15	3	3	7.2		1	
51	27	0120	13.8	19	2	2	8.2			
52		0240	13.2	29	16	16	12.3			
53		0410	13.2	42	35	15	11.0		1	
54		0645	14.2	7	0					
55		1340	14.5	10	0					
56		1450	14.6	20	0					
57		1600	14.5	7	0					
[1]58		1610		30	0					
59		1839	14.1	27	5	4	9.8	1		2
60		2115	14.0	17	3	3	12.8		1	
61		2330	13.8	12	1	1	11.7			
62	28	0145	14.4	15	11	7	9.4			
63		0415	15.2	5	42	14	7.1			
64		0640	15.2	2	22	15	6.9	1		

[1]Taken at same location as preceding tow at almost twice the depth.
[2]Number estimated from count of a substantial fraction.

mummichog, *Fundulus heteroclitus*, up to 8 days resulted in a decrease in the quantity of lipid droplets in cells of the digestive tract and contraction of the intestine such that the lumen was small, sometimes scarcely traceable (Ciullo 1975). While these considerations suggest that disease could be the cause of the midgut anomaly present in certain of the ocean-caught northern anchovy larvae, starvation is the more tenable explanation because there was no evidence of parasites or pathogens in the hematoxylin- and eosin-stained specimens, and other anomalies in these specimens were consistent with demonstrated effects of starvation.

Other Organs

Deterioration was sometimes evident in other organs, particularly in the specimens with the most severe anomalies in the musculature and digestive tract. The pancreas and liver, for example, showed good integrity in most larvae (Figures 1, 9), but some showed an unusual degree of dissociation in these organs (Figures 8, 10), and in a few, both organs had undergone considerable lysis. The kidney ducts were intact in all specimens, but in a few the cells of the ducts were unusually thin, or necrotic (Figure 12). In several the mantle layer of the brain showed poor integrity, perhaps from a reduction of neuroglia.

Classification of Larvae

During the course of microscope examination, each larva was designated healthy, incipient emaciation, moderate emaciation, or severe emaciation. The three classes pertaining to larvae with anomalies are not rigorous, but they imply the following: incipient, slight looseness of the trunk muscles; moderate, obvious separation of the trunk muscle fibers, some irregularity of the notochord and possibly the foregut, strong contraction of the midgut, and sometimes a high incidence of hypertrophic cells in the midgut mucosa; and severe, obvious separation and hyalinization, and sometimes disarray, of the muscle fibers, notable irregularity in the profile of the notochord and foregut, depletion of foregut muscosa cells, and fragmentation of midgut mucosa, with a central core of dissociated and necrotic cellular debris. Of the 318 larvae sectioned, 26 were classified as severely or moderately emaciated, and another 11 were classified as incipient. These are listed by net tow in Table 1 along with the raw data for all tows. The larvae classified as incipient are included with the healthy rather than with the emaciated or "starving" group in the sections that follow.

Relation of Emaciated Larvae to Other Variables

Standard Length

Emaciated larvae were all <10 mm SL and were distributed almost proportionately over the range 2-10 mm SL (Table 2). Larvae classified incipient were similarly distributed. In the lowest size category, 2.1-4.0 mm SL, only half of the 46 larvae examined had exhausted their yolk and become vulnerable to starvation. The emaciated individuals were part of this contingent. The absence of emaciated larvae in the categories above 10 mm SL may be a chance result of the relatively fewer numbers of larger larvae present in the tows, but there may also be some actual reduction in starvation effects at this size because of increasing lipid reserves with growth (Love 1974).

TABLE 2.—Standard length distribution of the northern anchovy larvae sectioned and examined and of those classified as emaciated or incipient.

Standard length	Number examined	Number emaciated	Number incipient
2.1- 4.0	46	6	3
4.1- 6.0	137	8	3
6.1- 8.0	60	8	3
8.1-10.0	30	4	1
10.1-12.0	26		1
12.1-14.0	14		
14.1-16.0	3		
16.1-20.0	3		

Geographical Distribution

More than half of the tows were spread over a large offshore area where abundance of northern anchovy larvae was generally low (Figure 13, Table 1) and where samples from six tows each contained a single emaciated larva. The remainder of the tows occurred in an area of a few hundred square miles off Newport Beach where larval abundance was high (Figure 14, Table 1) and where samples from four tows each contained several emaciated larvae. The fact that these four samples showed a high proportion of emaciated larvae, while others from nearby tows showed only healthy larvae, indicates that there was a contagious or patchy distribution of such larvae off Newport Beach.

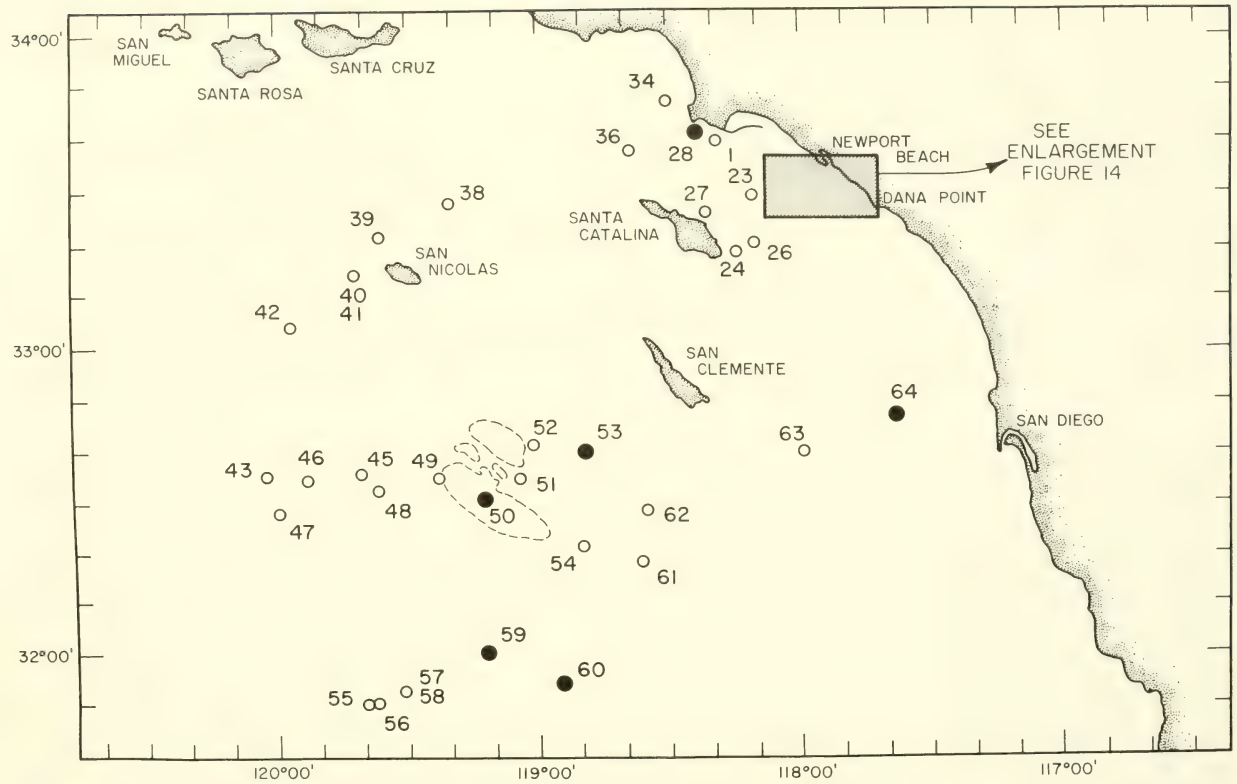


FIGURE 13.—The locations and sequence numbers of tows taken in March 1977 over the Southern California Bight, exclusive of the Newport Beach area. Open circles indicate tows from which all sectioned larvae were healthy, and dots indicate tows in which one of the sectioned larvae was emaciated. See Table 1 for data on tows.

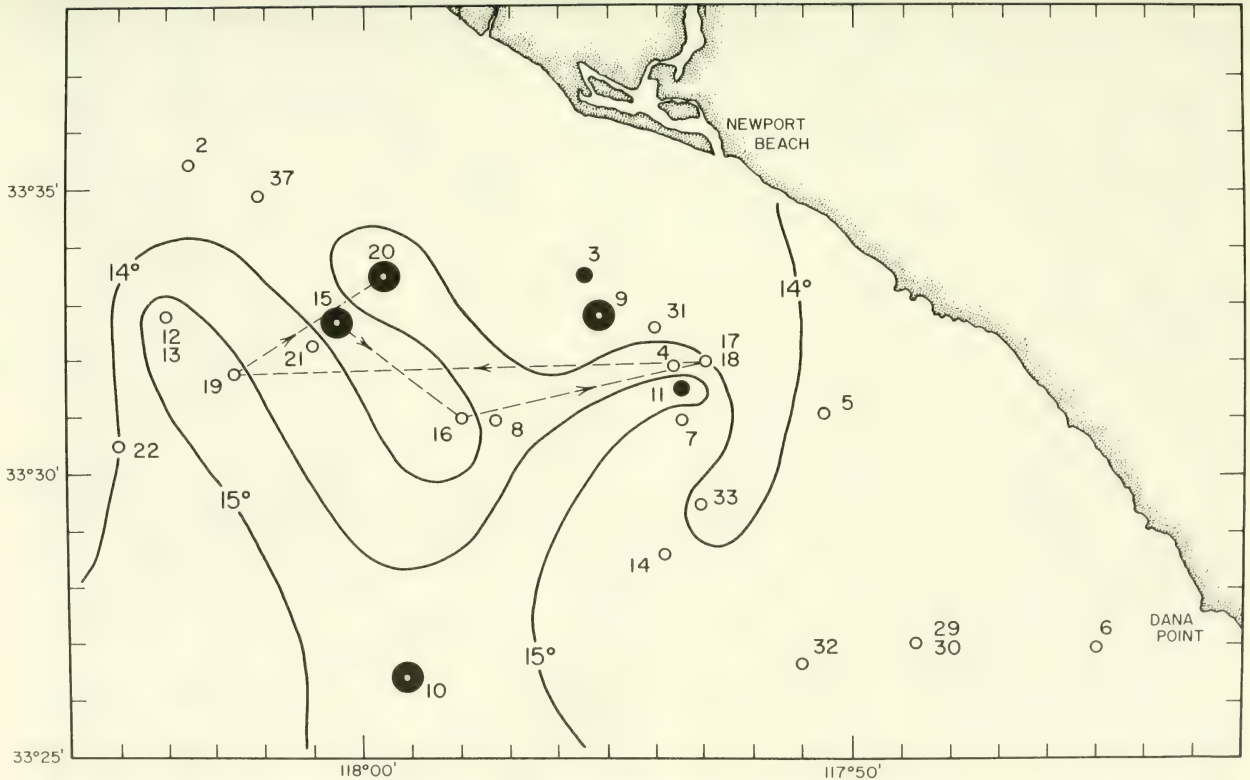


FIGURE 14.—The locations and sequence numbers of tows taken in the Newport Beach area, southern California. Open circles indicate tows from which all sectioned larvae were healthy; dots indicate tows from which one of the sectioned larvae was emaciated; larger dark circles with open centers indicate tows from which most of the sectioned larvae were emaciated; 1° C surface isotherms show that there was considerable temperature variation in the area; and dashed line is the cruise track for one 24-h period, and it indicates that the presence of emaciated larvae (tows 15 and 20) was persistent over at least this time span. See Table 1 for data on tows.

The impression of "patches" of larvae in poor condition indicated by the histological samples from the Newport Beach area was further strengthened by subsequent examination of the unsectioned larvae remaining from all net tows. Figure 15 shows a random portion of tow 23, which contained over 300 larvae and produced only healthy larvae in the histological sampling. The specimens are full-bodied with good symmetry and are straight, or at worst gently curved. Figure 16 shows a random portion of tow 9, which produced a high proportion of emaciated larvae in the histological sampling. Several of these larvae have angular body bends, trunks and digestive tracts that are lumpy and sinuous, and heads often misshapen with loose or missing eyes. They also appeared to be less intensely colored by the fixing solution than the others. When viewed in toto, this and the other three tow collections of larvae that produced histologically poor samples were readily distinguishable from all others.

The emaciated larvae consititute a percentage of the number of larvae examined, but the magnitude of this percentage depends on the portion of the total samples that are considered (Table 3). The four tows with a high incidence of emaciation, considered by themselves, indicate 60% emaciated larvae within local patches. This drops sharply to 12% when coverage is expanded to a few dozen tows in approximately 200 mi² off Newport Beach, and to 10% when an additional 10 tows, rather widely scattered over the San Pedro Channel area are included (inshore set). By comparison, the pooled offshore samples (offshore set) which represent perhaps 6,000 mi², indicate 5% emaciated, and samples pooled for the entire cruise show an intermediate value of 8% emaciated.

Day and night subsets of the inshore and offshore sets show differences in both the available population and the percentage of emaciated larvae. The lower daytime catches imply that the population was less available during this period, probably because much of it migrated below the 20 m depth of the tows during the day and probably also because larvae have some success in visually avoiding the net during the day. As a simple binomial function, the 15% emaciated larvae for the inshore night group is significantly higher

FIGURE 15.—A random portion of the northern anchovy larvae from tow 23, in which the larvae show generally good body form.

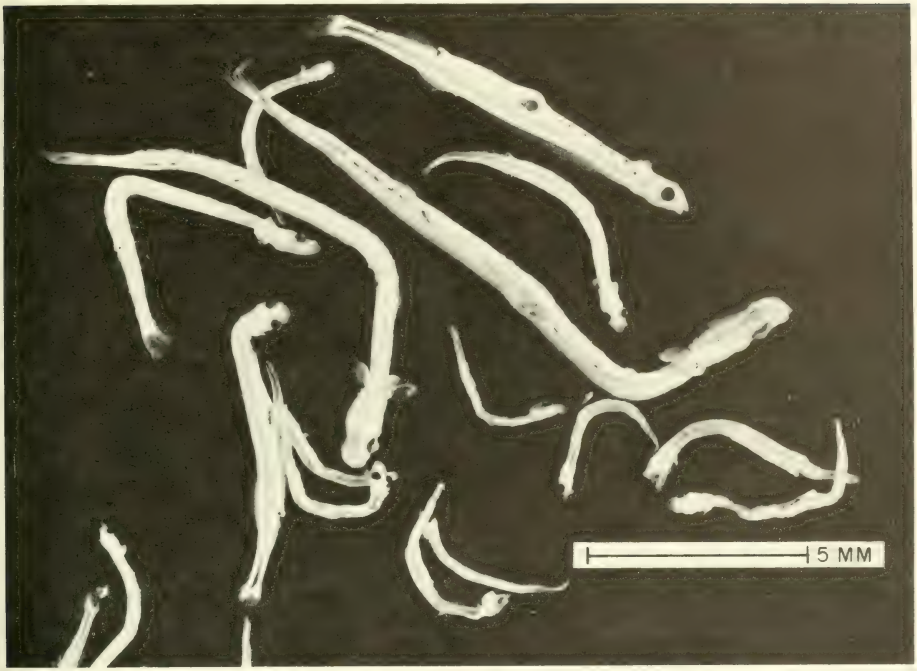


FIGURE 16.—A random portion of the northern anchovy larvae from tow 9, in which the larvae show generally irregular body form.

TABLE 3.—Percentage of emaciated northern anchovy larvae for different sample arrays.

Sample arrays	Number of tows	Larvae/ tow	Number of larvae examined	Number of larvae emaciated	Percent emaciated	95% confidence limits
Samples with high incidence of emaciation	4	37.5	30	18	60.0	±17.5
200 mi² coastal area includes above	27	77.1	165	20	12.1	± 5.0
Inshore set (tows 1-37):						
Day (0600-1800 h)	20	36.6	111	4	3.6	± 3.5
Night (1800-0600 h)	17	134.0	109	17	15.6	± 6.8
Pooled	37	81.3	220	21	9.6	± 3.9
Offshore set (tows 38-64):						
Day (0600-1800 h)	14	1.9	19	1	5.3	±10.0
Night (1800-0600 h)	13	11.2	79	4	5.1	± 4.8
Pooled	27	6.3	98	5	5.1	± 4.4
Total cruise pooled	64	50.0	318	26	8.2	± 3.0

than the other three subset percentages, but the obvious contagious nature of the distribution of these larvae casts doubt on the value of such tests. It is probably safer here to choose a lower percentage, such as the 8% for the entire cruise pooled, as representative, and assume that the observed subset differences are nothing more than sampling variation.

Surface Temperature

The tows with a high incidence of emaciated larvae were not associated with a given level of temperature, but it appears that they were located in an area of variable temperature (Figure 14). The 13° and 15° C tongues of water may have been basically persistent water masses, as Methot and

Kramer (1979) suggested, but the irregularity of the isotherms defining these tongues off Newport Beach implies local shifting of temperatures. Comparison of time as well as temperature differences along and adjacent to the cruise track for 20 March indicates, in fact, that notable temperature differences between closely located tows were probably more a matter of change over time than of static gradients between locations. Tows 15 and 20 are of particular interest because they both had a high incidence of emaciated larvae and were close together, but differed in temperature by 1.5° C. However, tow 20 was taken 24 h later than tow 15, and the thermograph record showed that the higher temperature applied to tow 15, as well as to the tow 19 and tow 20 positions, at the later time. Such short-term temperature shifts indicate that there was water mass instability or movement in the area.

Plankton Volume

Plankton volume averaged appreciably lower for the four tows with a high proportion of emaciated larvae than for either the inshore or the offshore set of tows (Table 4). The average number of larvae was also relatively low in these four tows, being about half the average for all tows off Newport Beach, or in the San Pedro Channel area (inshore set). Number of larvae and plankton volume, in fact, tend to be associated for the inshore set (Figure 17), and while the four tows with high incidence of emaciated larvae do not show the lowest values, they are among the tows with low values.

Plankton volume did not relate to temperature in the inshore area, but there were some interesting changes with time (Figure 18). From 17 March to midnight of 20 March all volumes were 11 ml or less. This includes the four tows with a high incidence of emaciated larvae, one of which (tow 20) was the last taken in this time period. Twenty-four hours later tow 21, the first tow with a markedly higher volume (21 ml), was taken at a nearby position (Figure 14). Three more tows of progressively higher volume were taken during night hours over the next few days, but there were also several tows with lower volumes (3-14 ml) taken during this period, some at night. This pattern indicates that there was a striking change in the plankton regime off Newport Beach starting on 21 March, with volume tending to be higher, especially at night, than it had been during the preced-

TABLE 4.—Mean plankton displacement volume (milliliters) for different sample arrays in the study of northern anchovy larvae off southern California.

Item	No. of tows	Larvae/ tow	Plankton Volume/ tow	Plankton SD
Samples with high incidence of emaciation	4	37.5	3.8	0.5
200 mi² coastal area includes above	27	77.1	8.3	9.3
Inshore set includes above	37	81.3	8.7	9.0
Offshore set	27	6.3	19.7	20.1
Total cruise	64	50.0	13.3	15.6

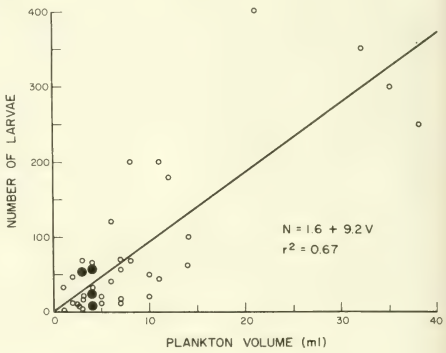


FIGURE 17.—The regression of number of anchovy larvae on displacement volume of plankton (larvae excluded) for the inshore tows, 1-37. The solid circles indicate the four tows with a high incidence of emaciated larvae.

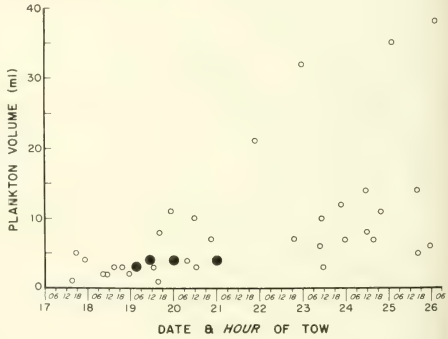


FIGURE 18.—Displacement volume of plankton on date (March 1977) and hour of tow. Dots indicate the four tows with a high incidence of emaciated larvae. Dates are in bold type and located at midnight points on the hour scale.

ing few days, when the tows with a high incidence of emaciated larvae were taken.

DISCUSSION

The most significant result of this study is that northern anchovy larvae showing symptoms indicative of starvation were indeed found in the ocean and were thus identified on the basis of their individual appearance. The emaciated condition of these larvae is very similar to that induced in laboratory animals by total food deprivation (O'Connell 1976), which implies that circumstances of insufficient food were responsible for their occurrence in the ocean, especially where samples contained many such larvae, as off Newport Beach. Other causes are possible, and one of the most obvious is discharge from sewage outfalls in the area. However, the discharges are now diffused rapidly and in general appear to be harmless and perhaps even beneficial to nearby young and adult fish (Southern California Coastal Water Research Project[3]).

Zones of insufficient food might well have existed in the Newport Beach area at the time of the survey. The variations in both temperature and plankton volume, which were clearly dynamic in nature, indicate that there was appreciable water mass movement or instability, and such conditions can alter plankton abundance. Lasker (1975, in press) found, for example, that phytoplankton blooms believed to be advantageous for first feeding anchovy larvae were variously dissipated and suppressed as the water column became unstable in turbulent weather and sea conditions. In the present study the time sequence of plankton volume change off Newport Beach shows the possibility that water with relatively low plankton levels and "patches" of emaciated larvae was being replaced by water with greater plankton abundance, in which larvae were also more abundant and generally healthy.

Although the occurrence of zones of insufficient food is a reasonable hypothesis in regard to the "patches" of emaciated larvae off Newport Beach, it is not a plausible explanation for some of the other samples, where occasional emaciated individuals occurred among abundant healthy larvae. It can only be surmised that in any location, and despite generally good conditions, there will be some instances of starvation through detrimental combinations of genetic constitution, accident, and chance failure to capture food.

If circumstances of poor food availability are produced by water mass activity, as suggested above for the Newport Beach area, they are likely to be more or less transient phenomena, which raises the question of short-term susceptibility of northern anchovy larvae. Immediately after yolk absorption, northern anchovy larvae will survive only a day or two without food (Lasker et al. 1970), and they will show visible effects before dying (O'Connell 1976). Protein components are quickly affected because early postyolk-sac fish larvae have negligible lipid reserves (Ehrlich 1974), though such reserves obviously increase with growth and become a buffer against insufficient food (Love 1974). Even so, northern anchovy larvae of relatively large size, 35 mm SL, survived only 2 wk, on the average, after feeding was stopped, and during this period the average lipid content of living larvae was declining while mortality in the population was rising, with smaller individuals dying sooner than larger ones (Hunter 1976a). Since larvae examined in the present survey were appreciably smaller than the above, thus having lower lipid reserves, the signs of emaciation could have resulted from relatively few days of insufficient food.

Most of the larvae showing histological signs of emaciation in this study also showed signs of previous feeding, not by the presence of food residue, but rather by remnants of eosinophilic inclusion bodies in the hindgut mucosa cells. The starvation and previous feeding indications are not incompatible. Laboratory feeding studies have shown that growth, lipid content, and survival all decline quickly under limited or discontinued feeding (O'Connell and Raymond 1970; Hunter 1976a), and it is probable that histological signs of deterioration would also appear quickly, especially in early larval stages.

If, as proposed by Hjort (1914, 1926), the level of mortality suffered by the early feeding stages of fish populations is a decisive component of the prerecruitment mortality, some measure of that mortality should be a useful indicator of ultimate year class success. The proportion of larvae observed to be starving may be one such useful indicator: It is directly visible, and it may reflect a substantial part of total daily mortality. Zweifel and Smith (in press) have estimated average daily

[3]Southern California Coastal Water Research Project. 1978. The effects of the ocean disposal of municipal waste. Summary Report of the Commission of the Coastal Water Research Project, June 1978, 27 p. Filed at 1500 East Imperial Highway, El Segundo, CA 90245.

population abundance of larval anchovies by length and region for the 1967 through 1975 California Cooperative Oceanic Fisheries Investigations net tow data, and length dependent mortality rates were calculated from the abundance estimates. For larvae of 7.5 mm SL, which approximates the median length of those showing symptoms of starvation in the present study, the estimated average daily mortality rate in the San Pedro Channel area was 21%. If it is assumed that all larvae showing symptoms will die directly or indirectly from starvation, the observed 8% with symptoms in the March 1977 survey could indicate a net daily mortality from starvation of 8%, which is 40% of the average total daily mortality for this length group. If starvation tends to contribute this substantially to total mortality, variations in the proportion of larvae observed to be starving may relate reasonably well to the magnitude of ongoing total mortality and consequently to recruitment from the year class.

How well the proportion of starving larvae from a given sampling in 1 yr will predict the eventual recruitment of that year class will only be evident from correlation of the two variables for at least a few years. As for 1977, with a northern anchovy "starvation ratio" of 8%, there were indications that recruitment would be good. The winter and early spring were relatively mild, a condition conducive to development of high density patches of larval food organisms, particularly from dinoflagellate blooms (Lasker in press). Growth rate of northern anchovy larvae was also shown to be above average in the San Pedro Channel area for March 1977 (Methot and Kramer 1979). The above average growth rate may have been valid for much of the population developing in the region without applying to the patches of emaciated larvae, which were taken at different locations than the growth samples. Estimates from recent catch data indicate that the 1977 year class is of moderate size, as compared with the large 1976 and 1978 year classes and the small 1974 and 1975 year classes (J. S. Sunada[4]). Thus, to the extent that 8% starving larvae is a reliable estimate of that parameter for 1977 and to the extent that the parameter is associated with recruitment, both higher and lower occurrences of starving larvae are likely possibilities from future surveys.

[4]J. S. Sunada, Assistant Biologist, Marine Resources Region, California Department of Fish and Game, 350 Golden Shore, Long Beach, CA 90802, pers. commun. May 1979.

Reliability of the estimate of starving larvae is probably reasonably good for 1977 in that tows were most concentrated in a region of high abundance, but reliability in future sampling efforts could probably be improved by more diligent stratification in respect to population distribution. In addition to sampling at more than one point in time, an effective strategy might be to expand sampling in several areas that show high abundance, particularly of larvae under 10 mm SL, along a preplanned survey track. Expanding sampling in this way would likely result in a quantity of samples that would be formidable if analysis is entirely dependent on histological or physiological parameters. The distinctive appearance of the aggregated larvae from those few tows of the present survey that contained predominantly emaciated larvae, however, suggests that histological analysis can be greatly reduced.

Assuming that starvation of any consequence will occur in patches, a stereomicroscope scan of the total aggregation of larvae from each tow should suffice for the identification and enumeration of such patches, with histological processing reserved for selected verification. Undoubtedly some of the starving larvae that occur as scattered single cases would be missed under such a procedure, but this should have little effect on the overall estimate.

ACKNOWLEDGMENT

I would like to acknowledge the very able assistance of Pedro Paloma, who sorted and measured all the samples and prepared all the slides.

LITERATURE CITED

BLAXTER, J. H. S.
1971. Feeding and condition of Clyde herring larvae. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 160:128-136.

BLAXTER, J. H. S., AND G. HEMPLE.
1963. Influence of egg size on herring larvae (*Clupea harengus* L.). J. Cons. 28:211-240.

CIULLO, R. H.
1975. Intestinal histology of *Fundulus heteroclitus* with observations on the effects of starvation. *In* W. E. Ribelin and G. Migaki (editors), The pathology of fishes, p. 733-767. Univ. Wis. Press, Madison.

EHRLICH, K. F.
1974. Chemical changes during growth and starvation of herring larvae. *In* J. H. S. Blaxter (editor), The early life history of fish, p. 301-323. Springer-Verlag, Berl.

EHRLICH, K. F., J. H. S. BLAXTER, AND R. PEMBERTON.
1976. Morphological and histological changes during the

growth and starvation of herring and plaice larvae. Mar. Biol. (Berl.) 35:105-118.

HARTHOORN, A. M.
1977. Problems relating to capture. Anim. Regul. Stud. 1:23-46

HJORT, J.
1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer 20:1-228.
1926. Fluctuations in the year classes of important food fishes. J. Cons. 1:5-38.

HUNTER, J. R.
1976a. Culture and growth of northern anchovy, *Engraulis mordax*, larvae. Fish Bull., U.S. 74:81-88.
1976b. Report of a colloquium on larval fish mortality studies and their relation to fishery research, January 1975. U.S. Dep. Commer., NOAA Tech. Rep. NMFS Circ. 395, 5 p.

LASKER, R.
1975. Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. Fish. Bull., U.S. 73:453-462.
In press. Factors contributing to variable recruitment of the northern anchovy (*Engraulis mordax*) in the California Current: contrasting years, 1975 through 1978. *In* K. Sherman and R. Lasker (editors), Symposium on the early life history of fish, Woods Hole, April 1979. Rapp. P.-V. Reun. Cons. Int. Explor. Mer.

LASKER, R., H. M. FEDER, G. H. THEILACKER, AND R. C. MAY.
1970. Feeding, growth, and survival of *Engraulis mordax* larvae reared in the laboratory. Mar. Biol. (Berl.) 5:345-353.

LOM, J.
1970. Protozoa causing diseases in marine fishes. *In* S. F. Snieszko (editor), A symposium on diseases of fishes and shellfishes, p. 101-123, Am. Fish. Soc., Spec. Publ. 5.

LOVE, R. M.
1974. The chemical biology of fishes. Acad. Press, Lond., 547 p.

LOVE, R. M., I. ROBERTSON, AND I. STRACHAN.
1968. Studies on the North Sea cod. VI. Effects of starvation. 4. Sodium and potassium. J. Sci. Food Agric. 19:415-422.

MARGOLIS, L.
1970. Nematode diseases of marine fishes. *In* S. F. Snieszko (editor), A symposium of diseases of fishes and shellfishes, p. 190-208. Am. Fish. Soc., Spec. Publ. 5.

METHOT, R. D., JR., AND D. KRAMER.
1979. Growth of northern anchovy, *Engraulis mordax*, larvae in the sea. Fish. Bull, U.S. 77:413-423.

NAKAI, Z., M. KOSAKA, M. OGURA, G. HAYASHIDA, AND H. SHIMOZONO.
1969. Feeding habit, and depth of body and diameter of digestive tract of *shirasu*, in relation with nutritious condition. [In Jpn., Engl. abstr.] J. Coll. Mar. Sci. Technol., Tokai Univ. 3:23-34.

O'CONNELL, C. P.
1976. Histological criteria for diagnosing the starving condition in early post yolk sac larvae of the northern anchovy, *Engraulis mordax* Girard. J. Exp. Mar. Biol. Ecol. 25:285-312.

O'CONNELL, C. P., AND L. P. RAYMOND.
1970. The effect of food density on survival and growth of early post yolk-sac larvae of the northern anchovy (*Engraulis mordax* Girard) in the laboratory. J. Exp. Mar. Biol. Ecol. 5:187-197.

SHELBOURNE, J. E.
1957. The feeding and condition of plaice larvae in good and bad plankton patches. J. Mar. Biol. Assoc. U.K. 36:539-552.

TEMPLEMAN, W., AND G. L. ANDREWS.
1956. Jellied condition in the American plaice *Hippoglossoides platessoides* (Fabricus). J. Fish. Res. Board Can. 13:147-182.

THEILACKER, G. H.
1978. Effect of starvation on the histological and morphological characteristics of jack mackerel, *Trachurus symmetricus*, larvae. Fish. Bull., U.S. 76:403-414.

TIBBO, S. N., L. R. DAY, AND W. F. DOUCET.
1961. The swordfish (*Xiphias gladius* L.), its life-history and economic importance in the northwest Atlantic. Fish. Res. Board Can., Bull. 130, 47 p.

UMEDA, S., AND A. OCHIAI.
1975. On the histological structure and function of digestive organs of the fed and starved larvae of the yellowtail, *Seriola quinqueradiata*. [In Jpn., Engl. summ.] Jpn. J. Ichthyol. 21:213-219.

YASUTAKE, W. T.
1975. Fish viral diseases: clinical, histopathological and comparative aspects. *In* W. E. Ribelin and G. Migaki (editors), The pathology of fishes, p. 247-271. Univ. Wis. Press, Madison.

ZWEIFEL, J. R., AND P. E. SMITH.
In press. A time series of anchovy embryonic and larval mortality estimates with confidence limits on the estimates of abundance of all sizes and on the mortality rate. *In* K. Sherman and R. Lasker (editors), Symposium on the early life history of fish, Woods Hole, April 1979. Rapp. P.-V. Reun. Cons. Int. Explor. Mer.

TRANSPORTATION OF CHINOOK SALMON, *ONCORHYNCHUS TSHAWYTSCHA*, AND STEELHEAD, *SALMO GAIRDNERI*, SMOLTS IN THE COLUMBIA RIVER AND EFFECTS ON ADULT RETURNS

WESLEY J. EBEL[1]

ABSTRACT

Chinook salmon, *Oncorhynchus tshawytscha*, and steelhead, *Salmo gairdneri*, were captured at Little Goose Dam in the Snake River during their seaward migration and transported 400 km downstream to the lower Columbia River below Bonneville Dam. Their survival was increased from 1.1 to 15 times as compared with control fish which passed by seven mainstem low-level dams and reservoirs. Variations in survival were mainly dependent on species and environmental conditions in the river during the period fish were transported.

The homing ability of the adult fish was not significantly diminished; less than 0.2% of strays occurred among adult returns from groups transported. Transportation did not affect ocean age or size of returning adult steelhead, but ocean age of returning adult chinook salmon may have been affected. Steelhead returned to Little Goose Dam at a substantially higher rate (1.4-2.7%) than chinook salmon (0.1-0.8%) from groups transported. The timing of adult returns of both species to Little Goose Dam was not related to the time of capture and downstream release of smolts.

Salmonid populations of the Snake River and its Idaho tributaries have declined rapidly in recent years to the point that the very survival of some stocks is threatened. The total run (i.e., catch plus escapement) of chinook salmon, *Oncorhynchus tshawytscha*, attributable to the Snake River dropped from 120,000 adults in 1972 to 50,000 in 1974 (Raymond 1979). Similarly, the total run of steelhead, *Salmo gairdneri*, an anadromous form of rainbow trout, declined from 100,000 adults in 1972 to below 20,000 in 1974. The downward trend of the anadromous salmonid populations has been ascribed to losses of juvenile migrants at the series of eight dams (Figure 1) and associated reservoirs in the Snake and Columbia Rivers through which the smolts must pass on their way to the sea (Raymond 1979).

With the goal of protecting the migrants from the hazards of dams, a system for transporting smolts around the dams was investigated by the National Marine Fisheries Service. The juvenile migrants were collected from the Snake River at Little Goose Dam (the uppermost dam—Figure 1), transported around the entire series of dams, and released below Bonneville Dam (the lowermost dam) on the Columbia River. The effects of such transportation on the survival and catch of the fish and on the ability of the adults to "home" to their natal streams must be known if fishery agencies are to evaluate the transportation system as a practical means of protecting Snake River salmonid runs. The main objectives of the research at Little Goose Dam were: to determine the effect of transportation on homing and survival of juvenile chinook salmon and steelhead collected at Little Goose Dam and released at two locations downstream from Bonneville Dam and to compare these results with an earlier study done at Ice Harbor Dam (Ebel et al. 1973) where fish were

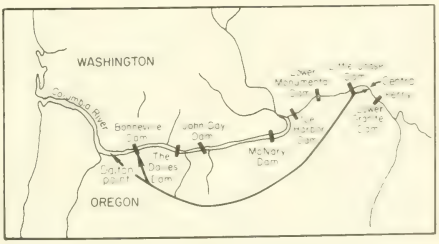


FIGURE 1.—Transportation routes and release location of experimental chinook salmon and steelhead collected and marked at Little Goose Dam, 1971-73.

[1]Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112.

Manuscript accepted December 1979.
FISHERY BULLETIN: VOL. 78, NO. 2, 1980.

transported a shorter distance. Secondary objectives were: to determine any relation between timing of downstream juvenile migrants and timing of subsequent adult returns and to determine whether size and ocean age of adults (transported as smolts) were affected by the collection and transport process. The results of the experiments described in this report are also compared with the preliminary results of the current experiment at Lower Granite Dam.

BACKGROUND

The changes in abundance and the causes of changes in abundance of individual salmonid populations in the Columbia River drainage have been summarized by Chaney and Perry (1976). Raymond[2] analyzed the trends in abundance of Snake River runs in detail and clearly showed that the major causes of the decline of the Snake River stocks are due to the losses of juveniles during their seaward migration. These losses are caused by injury or death occuring when the fish attempt to pass the eight dams and reservoirs placed in their migratory path. These dams now inundate over 630 km of the migratory route. The main causes of the juvenile losses have been attributed to: passage through turbines (Bell et al.[3]; Long, Krcma, and Ossiander[4]; Long, Ossiander, Ruehle, and Mathews[5]); supersaturation of river water with atmospheric gas (Ebel and Raymond 1976); delay in migration (Raymond 1968, 1969); and increased predation (Chaney and Perry 1976).

[2]Raymond, H. L. 1975. Snake River runs of salmon and steelhead trout: trends in abundance of adults and downstream survival of juveniles. Unpubl. manuscr., 11 p. Northwest and Alaska Fisheries Center, Natl. Mar. Fish. Serv., NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112.

[3]Bell, M. C., A. C. DeLacy, G. J. Paulik, and R. A. Winnor. 1967. A compendium on the success of passage of small fish through turbines. Northwest and Alaska Fisheries Center, Natl. Mar. Fish. Serv., NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112. (Contract DA-35-026-CIVENG-66-16, Report to U.S. Army Corps of Engineers, Portland, Oreg.)

[4]Long, C. W., R. F. Krcma, and F. J. Ossiander. 1968. Research on fingerling mortality in Kaplan turbines—1968. Unpubl. manuscr., 7 p. Northwest and Alaska Fisheries Center, Natl. Mar. Fish. Serv., NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112.

[5]Long, C. W., F. J. Ossiander, T. E. Ruehle, and G. M. Matthews. 1975. Final report on survival of coho salmon fingerlings passing through operating turbines with and without perforated bulkheads and of steelhead trout fingerlings passing through spillways with and without a flow deflector. Northwest and Alaska Fisheries Center, Natl. Mar. Fish. Serv., NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112. (Contract DACW68-74C-0113, Report to U.S. Army Corps of Engineers, Portland, Oreg.)

The National Marine Fisheries Service (NMFS) has been conducting transportation experiments since 1965 in an attempt to find ways of reducing these losses. The first study where natually migrating juveniles were collected and transported was conducted by Ebel et al. (1973). This study showed that the homing ability of adult spring and summer chinook salmon and steelhead captured during their seaward migration as juveniles and then transported downstream (from Ice Harbor Dam to below Bonneville Dam) was not diminished. Data based on returning adults indicated that survival rate of adult fish that had been transported as juveniles increased 1.5-3 times the survival rate of those not transported, depending on environmental conditions in the river during the time of transport. Studies conducted prior to this study with hatchery stocks of salmonids showed that the majority of the adult fish that had been transported as juveniles returned to the release site, not to the parent location (Snyder 1928; Ellis and Noble 1960). Obviously, juvenile salmonids captured during their seaward migration and then transported differed in their responses from fish transported directly from hatcheries. The wild and hatchery stocks captured in the experiment conducted by Ebel et al. (1973) were smolting and had traversed several hundred kilometers before capture. These may be the main factors causing the different response (homing ability was not diminished) obtained in the experiment done in 1973.

Previous experiments (Hasler and Wisby 1951; Groves et al. 1968; Scholz et al. 1973) on mechanisms used by fish for homing indicated that the experience prior to and during the time that a juvenile salmon migrates is important in enabling the fish to receive visual and olfactory cues necessary for homing as an adult.

Only a portion of the migration route was eliminated by transporting the fish from Ice Harbor Dam to The Dalles and Bonneville Dams. Elimination of this portion of the migratory route apparently did not seriously affect the ability of either the chinook salmon or steelhead to home. However, the length of the migration route or amount of homing cues that can be eliminated and still achieve satisfactory homing is unknown.

The success of the experiment by Ebel et al. (1973) at Ice Harbor Dam encouraged the NMFS to begin a similar experiment at Little Goose Dam in 1971. As this dam is approximately 130 km upstream from Ice Harbor Dam, an additional 130

km of the migratory route would be eliminated, and the fish would be intercepted during their juvenile migratory life stage about 2-3 wk earlier than they were at Ice Harbor Dam. The results achieved at this site could be quite different from those obtained at Ice Harbor Dam. To facilitate the collection of fish, an orifice bypass system, juvenile fish diversion screens, and raceways for collection of juvenile fish were built into Little Goose Dam during its construction. This system provided substantial numbers of fish for the experiment, but there was the possibility that these fish might be injured or stressed during the diversion and collection process.

TABLE 1.—Number of transported and nontransported (control) juvenile chinook salmon and steelhead that were marked and released from Little Goose Dam, 1971-73.

Species and release year	Control fish	Transported fish[1]	
		Dalton Point	Bonneville Dam
	No. released[2]	No. released[2]	No. released[2]
Chinook salmon:			
1971	20,673	30,637	35,252
1972	32,836	51,499	54,906
1973	88,170	57,758	83,606
Steelhead:			
1971	33,243	35,967	44,939
1972	32,488	22,831	27,326
1973	42,461	26,650	36,802

[1]Transported fish were released in the Columbia River at two sites downstream from Bonneville Dam: 2 km downstream on the Washington (side referred to in the table as Bonneville Dam) and 17 km downstream on the Oregon side at Dalton Point.
[2]Release totals adjusted for initial tag loss.

METHODS

Experimental Design

During the downstream migrations in 1971, 1972, and 1973 juvenile chinook salmon and steelhead were randomly selected from the raceways at Little Goose Dam and divided into three groups—one control and two transported groups. The adipose fin was removed from all experimental fish and each group was selectively marked with a thermal brand and magnetized wire tags. Thermal brands were changed every 5 d among all treatment groups except for the first 10-d marking period. During this period, marking continued for 10 d before a change was made. Codes for magnetized wire tags were changed yearly for each treatment group. The control group was released at Central Ferry, about 10 km upstream from Little Goose Dam; the transported groups were hauled in tank trucks to two locations downstream from Bonneville Dam (Figure 1). One release site was at Dalton Point, 17 km downstream from Bonneville on the Oregon side of the river; the other was at the Washington State boat launching site, about 2 km downstream from Bonneville Dam. Each year the goal was to mark at least 50,000 chinook salmon and 25,000 steelhead for each group. This goal was exceeded every year (Table 1) except for all groups of chinook salmon in 1971 and the control group of chinook salmon in 1972.

Collection and Marking of Fish and Fish Hauling Procedures

Juvenile chinook salmon and steelhead were collected at Little Goose Dam, using a fingerling collection and bypass system (Smith and Farr 1974). The system consisted of: 1) screens in the turbine intakes which diverted fish into the gatewells of each turbine intake; 2) a gatewell orifice and piping system which transported fish from the gatewells to a grader and counter; and 3) a fish grader and counter which sorted fish by size and electronically counted fish entering five raceways. When desired, fish could be diverted directly to the river—thus bypassing the grader, counter, and raceways.

Fingerling chinook salmon and steelhead were pumped with a 5-in Paco model fish pump into the marking building where they were anesthetized and sorted. Previously marked fish were returned to the river in the tailrace of the turbine discharge. Samples of at least 100 chinook salmon and steelhead were examined each day for percentage descaling to provide an index of fish condition. Any fish with >10% of the scales missing was considered descaled. Each of the remaining fish was cold-branded with liquid nitrogen (Park and Ebel 1974), had the adipose fin excised, and had a magnetic wire tag (Jefferts et al. 1963) inserted in the snout. Before passing into a transport truck, the fish went through a magnetic field and detection coil; an untagged fish was automatically rejected and returned to the marker for retagging. Initial tag loss was measured by examining samples of juveniles 48-72 h after tagging; subsequent tag loss was determined by examining returns of adult control and test fish at Rapid River Hatchery near Riggins, Idaho, and Dworshak National Fish Hatchery at Ahsahka, Idaho. A branded fish with an adipose fin clip that did not also have a coded

[6]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

wire tag was considered a fish that had lost its tag after marking. Steelhead and chinook salmon were kept in separate compartments in the tank truck whenever both species were hauled simultaneously. All fish were transported in a truck of 18,900 l (5,000 gal) capacity (Smith and Ebel 1973) that was equipped with aeration, refrigeration, and filtration systems. Load densities were governed by the size of the daily catch and were usually <0.12 kg/l (1 lb/gal) except during periods when unmarked fish were hauled. Maximum load density was kept <0.18 kg/l (1.5 lbs/gal) of water.

Water chemistry measurements were taken from the truck at the time of release for every load transported. Concentrations of ammonia, nitrogen, dissolved oxygen, carbon dioxide, pH, and total alkalinity were recorded for possible correlations with delayed mortality information. All releases were made at dusk. Records of mortality were kept during marking and at time of release; a sample of 50-100 fish was taken from each transported load and held for 48 h at Bonneville Dam to provide an indication of delayed mortality. This procedure was repeated during downstream migrations in 1971, 1972, and 1973.

Evaluation of Returning Adults

The effect of transportation on the survival and homing of adult fish was evaluated by comparing returns of transported and nontransported fish to the sport, commercial, and Indian fisheries in the lower Columbia River; to Little Goose Dam on the lower Snake River; to Rapid River Hatchery, Pahsimeroi Hatchery near Salmon, Idaho, and Dworshak Hatchery; and to the spawning grounds throughout the Snake River drainage.

All adult fish migrating upstream at Little Goose Dam must ascend one ladder located on the south side of the dam. An adult tag detection and fish separating device that intercepted tagged salmon and steelhead and diverted them into a holding pen was installed in this ladder in 1972 (Ebel 1974). Tagged fish from our study were readily identified by the missing adipose fin. All fish were anesthetized and further examined for brands. If the brand was recognizable, the origin of the fish could be determined without having to extract the magnetic tag from the snout.

Fish with recognizable brands were then weighed and measured, dart-tagged or jaw-tagged (Slatick 1976), and released to provide further information in the event of recapture upstream and to identify fish that fell back over the dam and ascended the ladder a second time. If a fish was known to be tagged but had a brand that was indistinguishable, it was held until maturity in holding tanks at the dam and artificially spawned. The tag was then extracted after spawning, and the test or control group was determined from the color code. Data obtained from these fish were combined with those obtained from reading brands.

The Columbia River gillnet fishery below Bonneville Dam, the Indian fishery above the dam, and the sport fishery (primarily below the dam) provided samples of chinook salmon throughout the spring run. The samples yielded information concerning the returns to the lower river of marked fish originating primarily in Idaho. Closure of the summer fishery on chinook salmon during all 3 yr and the spring fishery in 1974 and 1975 prevented sampling of this segment of the run in the lower river. The sport and commercial fisheries of the lower Columbia River and the sport fishery above Little Goose Dam provided samples of steelhead.

Surveys of spawning grounds were conducted with the cooperation of the Washington Department of Fisheries, Fish Commission of Oregon, and the Idaho Department of Fish and Game. Most of the surveys were in the Snake River drainage of Idaho, but hatcheries and spawning grounds of spring and summer chinook salmon in the upper Columbia River were also checked for strays.

The G statistic, Student's t-test, and analysis of variance were used for analysis of most return data.

RESULTS

Factors Influencing Assessment of Data

Tag loss, tag detector efficiency, transport mortality, and delayed mortality were factors that influenced the assessment of the experimental data. Comparisons of tests and control releases could be biased if a differential effect among any of these factors occurred between test and control releases and was not considered in the analysis. For example, if tag loss was greater in control releases than in test releases, percentage return would be biased in favor of the test release if the data were not adjusted for this loss.

During the 3 yr of this study, average annual initial tag loss ranged from 0.45% in 1973 to 10.4%

in 1972; average tag loss for the 3 yr of marking was 3.7%. Release totals were adjusted for initial tag loss. Additional tag loss (occurring after initial tag loss), based on examination of 884 marked adult steelhead at Dworshak National Fish Hatchery and 154 marked adult chinook salmon at Rapid River Fish Hatchery, was nill (<0.1%) and did not affect data analysis.

About 4-8% of the juvenile chinook salmon and 4-10% (Park et al.[7]) of the juvenile steelhead released as controls were recaptured and released at Little Goose Dam. No attempt was made to adjust the data for a small bias that might have occurred from this procedure. It was assumed that survival of this portion of the controls that were handled and released after passing through the collection system was the same or greater than survival of the majority of the control fish that had to pass either through the turbines or over the spillway.

The primary recovery site for evaluation of tag returns was at Little Goose Dam where an automatic tag detector and fish trap were installed (Ebel 1974). The efficiency of the detector and trap was based on a comparison of known recovery of fish with magnetized wire tags at Little Goose Dam and subsequent recovery of these and other marked fish at Rapid River and Dworshak Hatcheries. For example, 54 fish were identified at Rapid River Hatchery in 1975 from treatment groups that had passed Little Goose Dam. Of these, 50 had jaw tags indicating they had been captured and identified at Little Goose Dam; 4 did not have jaw tags indicating these fish had passed the dam without being trapped or identified. The trap efficiency for chinook salmon in 1975 was therefore 50/54 or 0.92. Thus, a factor of 1.08 was used to expand recoveries of .2- and .3-age[8] chinook salmon captured and identified at Little Goose Dam in 1975 from experimental releases in 1972 and 1973. Similar calculations were made for each year of recovery of chinook salmon during 1972-76 in computing estimated percentage return for a particular treatment group. The same procedure was used to estimate trap efficiency for steelhead with data obtained from recoveries at Dworshak Hatchery. The efficiency of recovery varied among years from 43 to 90% during the spring and summer when tagged chinook salmon were recovered. One source of variation was due to periodic shutdowns of the detector and trap for special studies of passage of adult fish. The efficiency remained constant (72%) during the fall of each year when most adult steelhead were recovered. An examination of the timing of test and control fish returning to Little Goose Dam indicated there was no significant difference. Thus, variations in efficiency did not affect comparisons of recoveries of test and control fish because all experimental groups passed the detector throughout the recovery period, and both test and control groups were subjected to the same variations in recovery efficiency. Total estimates of adult returns were adjusted for detector efficiency for a given period of recovery.

The use of the above method of estimating total percentage return for treatment groups assumes: loss of jaw tags from fish identified at Little Goose Dam was nil and jaw-tagged fish survived at the same rate as fish not jaw tagged. The first assumption is valid, I believe, because examination of several hundred fish at both Dworshak and Rapid River Hatcheries each year of recovery did not reveal any evidence of lost tags. Data from recent radio tracking studies (see Monan and Liscom[9]) suggest that the second assumption is also valid. In these studies, adult chinook salmon were obtained from the fish ladder with a similar trap and handled in an identical manner before tagging, and mortality of tagged fish was nil.

Transport mortality was defined as the mortality which occurred as a result of handling, marking, and hauling; delayed mortality was considered mortality that occurred in samples held at Bonneville Dam immediately after hauling. Transport mortality of both species was <1% of the total number of smolts handled (Table 2). Delayed mortality (Table 3) was considerably more, ranging from 10 to 22% for chinook salmon and 1.0 to 4.5% for steelhead. Transport and delayed mortality obviously reduced the total number of

[7]Park, D. L., J. R. Smith, E. Slatick, G. Matthews, L. R. Basham, and G. A. Swan. 1978. Evaluation of fish protective facilities at Little Goose and Lower Granite Dams and review of mass transportation activities, 1977. Northwest and Alaska Fisheries Center, Natl. Mar. Fish. Serv., NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112. (Contract DACW68-77-0043, Report to U.S. Army Corps of Engineers, Portland, Oreg.)

[8]Age designations follow the formulas of Koo (1962). The number of winters at sea is shown by an Arabic numeral preceded by a dot.

[9]Monan, G. E., and K. L. Liscom. 1974. Radio-tracking of spring chinook salmon to determine effect of spillway deflectors on passage at Lower Monumental Dam, 1973. Northwest and Alaska Fisheries Center, Natl. Mar. Fish. Serv., NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112. (Contract DACW57-73-F-0534, Final Report to U.S. Army Corps of Engineers, Portland, Oreg.)

TABLE 2.—Mean mortality of juvenile chinook salmon and steelhead during transport from Little Goose Dam to release locations downstream from Bonneville Dam, 1971-73.

Species	Percentage mortality		
	1971	1972	1973
Chinook salmon	0.87	0.57	0.70
Steelhead	0.16	0.51	0.51

TABLE 3.—Mean delayed mortality of samples of juvenile chinook salmon and steelhead taken from marked groups transported from Little Goose to below Bonneville Dam. Fish were held from 48 to 72 h after transport.

Species	Percentage mortality		
	1971	1972	1973
Chinook salmon	22.8	10.0	17.2
Steelhead	1.0	1.4	4.5

transported smolts released and correspondingly reduced adult returns from transported groups. Control groups may have been less affected because of the shorter transport time (1 h vs. 6 h). However, the assessment of benefits or losses obtained from transport of salmonid smolts must include this mortality. Release totals were therefore not adjusted for either transport or delayed mortality. It was noted that over 90% of the dead fish in the delayed mortality group had obvious signs of descaling or injury.

Measurements of descaling (fish with >10% of the body area descaled) of chinook salmon smolts that were recorded during the marking process varied from 0 to as high as 50% of the individuals observed. The average annual descaling rate was 16.6% in 1972 and 19.6% in 1973. Incomplete records of descaling measurements made it impossible to determine the average rate of 1971. Descaling of steelhead was substantially less than descaling of chinook salmon; the overall average for 1972 and 1973 was <1%. It was determined from other studies being conducted that most of the descaling was caused by experimental diversion screens being tested in the turbine intakes (Ebel et al.[10]).

There was a relation between descaling rate and delayed mortality. Steelhead were less descaled than chinook salmon and had much less delayed mortality than chinook salmon. It appears that if the injury that occurred during diversion and handling could be eliminated, survival of transported chinook salmon could be substantially improved.

Returns of Adult Experimental Fish to Little Goose Dam

A comparison of ratios of transport and control percentage returns of adults to Little Goose Dam from releases of chinook salmon and steelhead for the 3 yr of this study (Figure 2) indicated that survival of both species was substantially increased in 1973 by transporting the fish to the Dalton Point and Bonneville Dam release sites.

The percentage increase in survival varied from year to year and, I believe, was dependent primar-

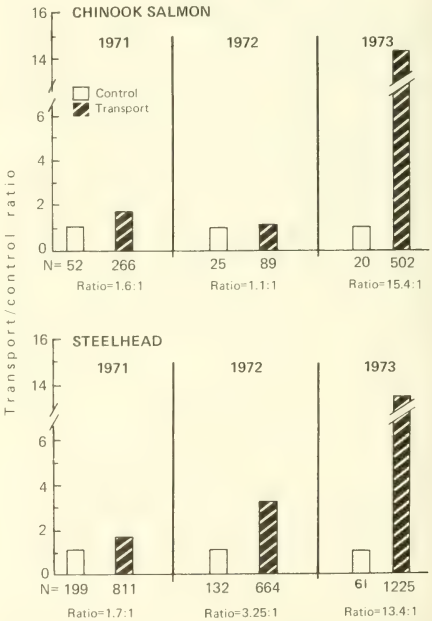


FIGURE 2.—Comparison of ratios of adult percentage return to Little Goose Dam from control and transported juvenile chinook salmon and steelhead. (Returns from Dalton Point and Bonneville Dam releases combined.) Percentage return of controls was set at unity for each year and species; the increase (transport percentage return ÷ control percentage return) is shown by darkened bar.

[10]Ebel, W. J., R. F. Krcma, and H. L. Raymond. 1973. Evaluation of fish protective facilities at Little Goose Dam and review of other studies relating to protection of other salmonids in the Columbia and Snake River, 1973. 62 p. Northwest and Alaska Fisheries Center, Natl. Mar. Fish. Serv., NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112. (Contract DACW68-71-0093, Progress Rep. to U.S. Army Corps of Engineers, Portland, Oreg.)

ily on river conditions. During years when survival of natural migrants (hatchery and wild stocks migrating naturally) was low, there was correspondingly low survival of control releases and greatest benefit from transportation. For example, in 1973, natural migrant survival estimates (Raymond 1979, see footnote 2) indicated an all-time low survival rate for both juvenile chinook salmon and steelhead migrants; in contrast, transport-control ratios were highest—15.4:1 for chinook salmon and 13.4:1 for steelhead (Figure 2). Raymond (1979) compared survival estimates of control releases from this study and other earlier studies (Ebel et al. 1973; Slatick et al. 1975) with survival estimates of naturally migrating smolts and found a high correlation ($r = 0.95$ for chinook salmon; 0.92 for steelhead) between survival of controls from transportation studies and his estimates of survival of natural migrants for the years 1968 to 1975. These data indicated there were close relationships between survival of releases of control fish marked for the transportation studies and hatchery and wild stocks migrating naturally. Raymond also correlated low survival with adverse river conditions; thus benefits from transportation would be highest when river conditions are the most adverse.

Statistical analysis of the return percentages (Table 4) was done by analysis of variance. A test of normality (Shapiro and Wilk 1965) of the percentage return data showed that the data were normally distributed ($P<0.05$); thus, transformation of percentage figures was not necessary. Analysis of variance of the return percentages indicated that the differences between "treatments" (test and control releases) were significant at the 1% level (Table 5). Interactions of the treatment × species were significant at the 5% level, indicating that the effects of treatment varied between chinook salmon and steelhead. For example, the mean transport/control ratio for returning chinook salmon in 1972 was 1.1:1, whereas the mean ratio for steelhead was 3.25:1. An analysis of the test of treatment effects—to compare the two downstream releases (both transported) and the control vs. the transported groups (Table 5)—clearly showed that there were no differences between recoveries from the Dalton Point and Bonneville Dam release sites and that the differences shown between test and control groups (Figure 2) were highly significant ($P<0.01$). Since interactions of the treatment × species were significant ($P<0.05$), I also analyzed the chinook salmon and steelhead percentages separately (Table 6). These analyses confirmed that differences shown between test and control groups were significant ($P<0.05$) for both steelhead and chinook salmon and that there were no differences between re-

TABLE 4.—Releases and recaptures of experimental fish.

Species, release site, and year	Number released	Ocean age[1] (no.) .1	.2	.3	Total	Adult returns (%) Observed	Estimated[2]	Transport/control ratio[3]
Chinook salmon[4]:								
Control:								
1971	20,673	5	28	19	52	0.252	0.470	
1972	32,836	4	12	9	25	0.076	0.106	
1973	88,170	2	11	7	20	0.023	0.026	
Transport:								
Dalton Point:								
1971	30,637	9	70	40	119	0.388	0.760	1.6:1
1972	51,499	4	20	20	44	0.085	0.114	1.1:1
1973	57,758	35	130	76	241	0.417	0.730	28.1:1
Bonneville Dam:								
1971	35,252	11	83	53	147	0.417	0.785	1.7:1
1972	54,906	5	28	12	45	0.082	0.110	1.0:1
1973	83,606	34	142	85	261	0.312	0.438	12.2:1
Steelhead:								
Control:								
1971	33,243	75	121	3	199	0.599	0.833	
1972	32,488	75	57	—	132	0.406	0.564	
1973	42,461	20	41	—	61	0.144	0.199	
Transport:								
Dalton Point:								
1971	35,967	124	237	6	367	1.020	1.418	1.7:1
1972	22,831	187	130	1	318	1.393	1.936	3.6:1
1973	26,650	276	276	5	517	1.940	2.698	13.5:1
Bonneville Dam:								
1971	44,939	166	287	11	464	1.033	1.436	1.7:1
1972	27,326	202	139	5	346	1.266	1.750	3.1:1
1973	36,802	352	353	3	708	1.924	2.673	13.4:1

[1]Age designation follows the formulas of Koo (1962). The number of years at sea is shown by an Arabic numeral preceded by a dot.
[2]Return percentage adjusted according to tag detector and trap efficiency.
[3]Transport/control ratios determined by dividing estimated percentage return of controls into estimated return of transported fish.
[4]Adult returns of spring and summer chinook salmon combined.

TABLE 5.—Analysis of variance of comparative percentage returns of adult chinook salmon and steelhead to Little Goose Dam for transported and nontransported (control) juveniles, 1971-73.

Source	df	SS	MS	Pooled residual (F)	Residual (F)
Treatments (test and control returns)	2	3.053	1.526253	8.924**	12.717**
Years (1971-73)	2	0.398	0.198794	1.162	1.657
Species (chinook and steelhead)	1	5.520	5.520057	32.276**	46.005**
Treatment × years	4	0.890077	0.223	—	1.858
Treatment × species	2	1.356179	0.678	3.965	5.650*
Years × species	2	0.698503	0.349	2.042	2.908
Residual	4	0.478141	0.120	—	—
Pooled residual	8	1.368218	0.171	—	—
Total	17	13.762118			
Partition of treatment SS (above), comparing adult chinook salmon and steelhead returns for control vs transport and Dalton Point vs. Bonneville Dam					
Control vs. transport	1	3.035	3.035	17.743**	
Bonneville vs. Dalton Point	1	0.018	0.018	0.105	

*$P < 0.05$; **$P < 0.01$.

TABLE 6.—Analysis of variance of comparative percentage returns of adult chinook salmon and steelhead to Little Goose Dam for transported and nontransported (control) juveniles, 1971-73 (returns analyzed by species).

Source	df	SS	MS	F
Chinook salmon return data				
Treatments (test and control returns)	2	0.179	0.089	2.70
Years (1971-73)	2	0.473	0.237	7.14*
Error	4	0.132	0.033	
Total	8	0.7849		
Partition of treatment sum of squares (above) comparing adult chinook salmon returns for control vs. transport and Dalton Point vs. Bonneville Dam.				
Control vs. transport	1	1.604	1.604	48.45**
Bonneville vs. Dalton Point	1	0.014	0.014	0.4342NS
Steelhead return data				
Source	df	SS	MS	F
Treatments (test and control returns)	2	4.230	2.115	6.845
Years (1971-73)	2	0.623	0.311	1.006
Error	4	1.236	0.309	
Total	8	6.089		
Partition of treatment sum of squares (above) comparing adult steelhead returns for control vs. transport and Dalton Point vs.Bonneville Dam.				
Control vs. transport	1	4.223	4.223	13.667*
Bonneville vs. Dalton Point	1	0.062	0.062	0.020NS

* = $P < 0.05$; ** = $P < 0.01$; NS = nonsignificance.

coveries from the Dalton Point and Bonneville Dam release sites for either chinook salmon or steelhead.

Percentage Adult Returns of Transported Releases

Analysis of the transport/control ratio provides the best insight as to the possible benefits from the transportation system, but total percentage return obtained from the groups transported must also be examined to accurately assess the effectiveness of the system as it operated. If both transport and control groups were excessively stressed during the diversion, collection, marking, and transport operations, then percentage returns would have been abnormally low even though transport/control ratios were favorable. I, therefore, compared percentage returns of the transport groups with percentage returns of production releases achieved at Dworshak and Rapid River Hatcheries and with estimated percentage returns of steelhead and chinook salmon to Little Goose Dam.

Returns from production releases of juvenile steelhead at Dworshak Hatchery (Olson[11]) were 0.25% in 1971, 0.20% in 1972, and 0.052% in 1973. Corresponding estimated percentage returns of steelhead from those transported from Little Goose Dam in 1971, 1972, and 1973 (returns from Dalton Point and Bonneville Dam releases combined) were 1.4, 1.8, and 2.7%, respectively. Although the sport fishery for steelhead above Little Goose Dam in 1973 would have reduced the percentage returns to Dworshak for releases in 1971, the estimated catch of 2,459 (Petit[12]) when added to the total hatchery returns, resulted in a return percentage of <0.50 for the 1971 release. The sport fishery was closed from 1974 to 1976; thus returns from releases in 1972 and 1973 at Dworshak Hatchery were not affected.

I also compared percentage adult returns of steelhead with the estimated percentage adult returns from populations of natural migrants passing Little Goose Dam in 1971, 1972, and 1973 by Raymond (1979, see footnote 2). His estimates of percentage returns were based on counts of adults passing the dam and estimates of populations of smolts (both hatchery and wild) passing Little Goose Dam for a given year. His estimates of percentage adult returns of steelhead to Little Goose

[11]Wayne Olson, Hatchery Manager, Dworshak National Fish Hatchery, Ahsahka, Idaho, pers commun. 1973-76.

[12]Steven Petit, Senior Fisheries Research Biologist, Idaho Fish and Game Dep., Lewiston, Idaho, pers. commun. June 1974.

Dam for 1971, 1972, and 1973 were 0.8, 0.4, and 0.2%, respectively. These estimates did not include fish that were transported. A substantial increase in survival of transported steelhead is indicated by both analysis of test/control ratios and comparisons of percentage returns of adults from transported groups with percentage returns of adults to Dworshak Hatchery and Little Goose Dam.

Percentage returns from production releases of juvenile chinook salmon to Rapid River Hatchery (Parrish[13]) in 1971, 1972, and 1973 were 0.59, 0.12, and 0.15%, respectively. The corresponding percentage returns from juvenile chinook salmon transported from Little Goose Dam were 0.77, 0.11, and 0.52%, respectively. Estimated adult returns (Raymond 1979, see footnote 2) of the mixture of wild and hatchery populations of juvenile chinook salmon passing Little Goose Dam in 1971, 1972, and 1973 were 1.3, 0.6, and 0.4%, respectively. While some benefit can be shown when percentage return data from transported groups are compared with only the Rapid River Hatchery returns for 1971 and 1973, only those transported in 1973 showed a benefit when returns were compared with estimated percentage returns of adults from mixed wild and hatchery smolts passing Little Goose Dam.

When the combined returns of spring and summer chinook salmon were divided into seasonal races (Table 7) and compared for the 3 yr of this study, the benefits or losses from transportation were defined by time. Transport/control ratios indicated that spring chinook salmon received greater benefit from transportation in 1971 and 1973 than summer chinook salmon. Summer chinook salmon appeared to receive more benefit than spring chinook salmon in 1972, but returns from all chinook salmon releases were low in 1972.

Several factors could be responsible for the differential in transport/control ratios between spring and summer chinook salmon among the years. Probably the most important factor was the timing of seaward migration of the two races of salmon. The race migrating downstream during the most favorable river conditions would receive the least benefit from transport in any particular year.

[13]Evan Parrish, Hatchery Manager, Idaho Fish and Game Dep., Rapid River Hatchery, Riggins, Idaho, pers commun. 1973-76.

Timing of Adult Returns of Chinook Salmon

Analysis of data on timing of adult returns in comparison with timing of the juvenile seaward migration (Table 8) indicated that the timing of adult returns of chinook salmon to Little Goose Dam was independent of timing of juvenile seaward migration ($G = 0.518, 0.516$, and 0.293: $df = 1, P < 0.05$ for 1971, 1972, and 1973, respectively). This is in contrast to what Ebel et al. (1973) found in adult chinook salmon returning from groups marked at Ice Harbor Dam in 1968. In this study most of the chinook salmon marked early in the spring migration returned early as spring chinook salmon, and most of those marked late returned later as summer chinook salmon. Perhaps intercepting the fish 130 km farther upstream eliminated the relation indicated from the earlier study. It is also possible that races of chinook salmon that exhibited this behavior in 1968 were absent or very low in numbers during 1971-73.

TABLE 8.—G-statistic test of relationship between timing of adult returns of chinook salmon to timing of juvenile seaward migration at Little Goose Dam, 1971-73.

Juvenile migration		Adult returns				
Year	Period[1]	Spring[2] (no.)	Summer[3] (no.)	Total (no.)	G	Significance[4]
1971	Early	73	25	98		
	Late	120	33	153		
	Total	193	58	251	0.518	NS
1972	Early	22	23	45		
	Late	14	10	24		
	Total	36	33	69	0.516	NS
1973	Early	149	86	235		
	Late	122	63	185		
	Total	271	149	420	0.293	NS

[1]Early = marked as juveniles from beginning of migration to 5 May. Late = marked as juveniles after 5 May.
[2]Prior to 15 June.
[3]After 14 June.
[4]$P > 0.05$, $df = 1$; NS (nonsignificance) indicates timing of adult returns is independent of timing of seaward migration.

TABLE 7.—A comparison of adult returns to Little Goose Dam of transported and nontransported (control) spring and summer chinook salmon smolts, 1971-73. Percentage values indicate adult returns from transported group.

Seasonal race of chinook	1971					1972					1973				
	Control		Transport		Ratio transport: control	Control		Transport		Ratio transport: control	Control		Transport		Ratio transport: control
	No.	%	No.	%		No.	%	No.	%		No.	%	No.	%	
Spring	37	0.179	200	0.303	1.70:1	18	0.055	65	0.061	1.1:1	10	0.011	329	0.232	21.2:1
Summer	15	0.073	66	0.100	1.37:1	5	0.009	24	0.022	2.4:1	10	0.011	161	0.114	10.4:1

Size and Years-in-Ocean of Adult Experimental Fish

Since transported fish (chinook salmon and steelhead) had the opportunity to enter the ocean more than 1 mo earlier than control fish that migrated naturally, the size and ocean age of returning adults were examined to determine whether a difference existed. The average weights of chinook salmon and steelhead released as controls were compared with the average weights of transported groups returning at the same ocean age. A paired comparison t-test using the data from Table 9 showed no significant differences in average weights for chinook salmon and steelhead (chinook salmon: $t = 0.315, P>0.5$; steelhead: $t = 0.297, P>0.5$ df = 8).

The ratio of age .3 to age .2 chinook salmon and the ratio of age .2 to age .1 steelhead were compared (Table 10) between transported and control groups. These comparisons indicated whether transporting affected the time that fish spent in the ocean before their return to Little Goose Dam. An analysis of variance of the ratios for the 3 yr of the study (Table 11) showed that the differences in ocean age between transported and control steelhead were not significant ($P<0.05$). A significant ($P<0.05$) difference in ocean age between control and transported chinook salmon did occur with a slightly higher ratio of .3/.2-age chinook salmon indicated among control returns. By these analyses, the transportation of smolts to locations downstream from Bonneville Dam was not shown to influence either the age or size of returning adult steelhead but may have influenced age of returning adult chinook salmon.

TABLE 9.—Average weights (kilograms) of returning chinook salmon and steelhead to Little Goose Dam from control (C) and transported (T) releases of smolts, 1971-73.

Species and year of release	Jacks		2-yr-in-ocean fish		3-yr-in-ocean fish	
	C	T	C	T	C	T
Chinook salmon:						
1971	1.66	1.40	5.06	4.74	8.22	9.20
1972	1.41	1.39	4.19	4.28	10.08	9.27
1973	1.86	1.51	4.40	4.46	7.77	9.02
Steelhead:						
1971	2.42	2.37	5.80	5.16	6.19	5.75
1972	2.39	2.53	4.38	4.24	4.44	4.84
1973	2.32	2.25	4.47	4.73	3.74	4.70

TABLE 10.—Comparison of transport and control age ratios on adults returning to Little Goose Dam, 1971-73. Chinook salmon age .3/.2 and steelhead age .1/.2 were used to determine ratios.

Year	Control			Transported		
	Ocean age[1] (no.)			Ocean age[1] (no.)		
	.2	.3	Ratio	.2	.3	Ratio
Chinook salmon:						
1971	28	19	0.68	153	93	0.61
1972	12	9	0.75	48	32	0.67
1973	11	7	0.64	272	161	0.59
	.1	.2		1	2	
Steelhead:						
1971	75	121	1.61	290	524	1.81
1972	75	57	0.76	389	269	0.69
1973	21	41	1.95	628	629	1.00

[1]Age designation follows the formulas of Koo (1962). The number of years at sea is shown by an Arabic numeral preceded by a dot.

TABLE 11.—Analysis of variance of ratios of ocean age .3 to .2[1] chinook salmon and age .2 to .1 steelhead adults returning to Little Goose Dam from transported and control releases.

Species	Source	df	SS	MS	F
Chinook salmon	Treatments (transport and controls)	1	0.00657	0.00657	23.6*
	Years (1971-73)	2	0.00931	0.00465	33.3*
	Error	2	0.00394	0.000197	
	Total	5	0.016274		
Steelhead	Treatments (transport and controls)	1	0.114	0.114	0.633NS
	Years (1971-73)	2	1.058	0.529	2.94NS
	Error	2	0.359	0.180	
	Total	5	1.532		

*$P<0.05$.

[1]Age designation follows the formulas of Koo (1962). The number of winters at sea is shown by an Arabic numeral preceded by a dot.

Recovery of Marked Chinook Salmon in the Commercial and Sport Fisheries

The experimental plan to evaluate recoveries of adult chinook salmon in the commercial, Indian, and sport fisheries required sampling of these fisheries each year from 1973 to 1975. However, the spring chinook salmon run began a rapid decline in 1973, which forced the commercial fishery to close in 1974 and 1975. As a consequence, sufficient data on chinook salmon were obtained only in 1973 for comparison of transported and control recoveries. A test fishery was conducted in 1974 and 1975, but only 18 salmon were recovered from the experimental releases during these years—too few to make comparisons of recoveries. Sixty-one salmon (Table 12) were recovered in 1973 from the 1971 experimental releases. The combined transport/control ratio of these recoveries, computed after adjusting the number of juveniles released, indicated that chinook salmon transported as juveniles were captured at 2.86 times the rate of control fish. This is a substantially higher test/control ratio than the 1.6:1 computed for returns to Little Goose Dam, indicating that transported groups were captured at a higher rate in the fishery than at Little Goose Dam. This

TABLE 12.—Comparison between transported and nontransported (control) chinook salmon of 1971 that were captured during 1973 as adults in the commercial, Indian, and sport fisheries in the lower Columbia River. (Numbers observed, not estimated.)

	Transported					
	Dalton Point		Bonneville Dam		Control	
	Recaptures		Recaptures		Recaptures	
Item	No.	%	No.	%	No.	%
Upstream from Bonneville Dam (Indian fishery)	14	0.046	14	0.040	4	0.019
Downstream from Bonneville Dam (commercial and sport fisheries)	9	0.029	18	0.051	2	0.010
Total	23	0.075	32	0.091	6	0.029
Combined recoveries (Dalton Point and Bonneville Dam)[1]				0.083	6	0.029

[1]Transport/control ratio = 2.86:1.

suggests that perhaps the adult fish from transported stocks were spending a longer time in the lower river, thus allowing a greater catch of these groups.

Recovery of Marked Steelhead in the Indian and Sport Fisheries

The Indian fishery of the lower Columbia River in 1973 and 1974 was not sampled because of closures during most of the season. However, in 1975 a substantial fishery was in progress. Sampling of this fishery yielded 39 marked steelhead from 1973 experimental releases. Thirty-eight of these were from transported groups; only one fish of a control group was recovered. The ratio of transport to control was 30:1, again indicating a higher catch rate of transported steelhead in 1973 than was recorded at Little Goose Dam where the transport/control ratio was 13.4:1.

TABLE 13.—Recoveries of adult steelhead from the sport fishery upstream from Little Goose Dam. Juveniles were released, 1971-73, as controls at Central Ferry; transported groups were released at Dalton Point and Bonneville Dam.

	Control		Transported groups		
Year released	No. of fish	Percentage return	No. of fish	Percentage return	Transport/control ratio[1]
1971	50	0.150	149	0.184	1.2:1
1972	24	0.074	63	0.126	1.7:1
1973	0	—	24	0.037	—
Total	74		236		

[1]Transport/control ratios computed from the combined recoveries of the Bonneville Dam and Dalton Point releases.

The sport fishery upstream from Little Goose Dam in the Snake River was intensive in 1972 and 1973 but was closed for a portion of 1974. Sampling of this fishery yielded 310 marked steelhead (Table 13) from experimental releases in 1971-73. The transport/control ratio estimated from these recoveries indicated a benefit from transport, but the benefit was about half that indicated downstream at Little Goose Dam from releases in 1971 and 1972. The benefit was substantial in all recovery locations from releases in 1973.

Returns of Adult Experimental Fish to Hatcheries and Spawning Grounds

Spawning ground surveys and examination of adult fish in Idaho hatcheries provided further information concerning transport/control ratios of chinook salmon and steelhead at their "home" destination.

Adult chinook salmon returns were examined at Rapid River Hatchery; steelhead returns were examined at Dworshak National Fish Hatchery and at the Pahsimeroi Hatchery (Table 14). Ex-

TABLE 14.—Returns of adult chinook salmon and steelhead to hatcheries of the upper Snake River drainage, 1971-73.

		Released 1971			Released 1972			Released 1973		
		Recoveries		Transport/control ratio	Recoveries		Transport/control ratio	Recoveries		Transport/control ratio
Species and hatchery of origin	Release site and experimental group[1]	No	%		No.	%		No.	%	
Chinook salmon Rapid River	Bonneville Dam (T)	33	0.094	4.95:1	5	0.009	—	24	0.029	14.5:1
	Dalton Point (T)	25	0.082	3.32:1	7	0.014	—	42	0.073	36.5:1
	Total	58	0.088	4.63:1	12	0.011	—	66	0.047	23.5:1
	Central Ferry (C)	4	0.019		0	0	—	2	0.002	
Steelhead Dworshak	Bonneville Dam (T)	96	0.214	1.37:1	26	0.095	3.80:1	104	0.283	13.5:1
	Dalton Point (T)	49	0.136	0.87:1	17	0.074	3.00:1	114	0.428	20.4:1
	Total	145	0.179	0.87:1	43	0.086	3.44:1	218	0.344	16.4:1
	Central Ferry (C)	52	0.156		8	0.026		9	0.021	
Pahsimeroi	Bonneville Dam (T)	8	0.018	–	11	0.040	3.33:1	18	0.049	24.5:1
	Dalton Point (T)	5	0.014	—	9	0.039	3.25:1	18	0.068	34.0:1
	Total	13	0.016	—	20	0.040	3.33:1	36	0.057	28.0:1
	Central Ferry (C)	0			4	0.012		1	0.002	

[1]T = transported group; C = control.

cept for steelhead returns to Dworshak Hatchery from releases in 1971, transport/control ratios computed from these data indicated that the benefits from transportation were greater than those indicated from returns to Little Goose Dam.

This was particularly evident in returns of chinook salmon and steelhead from releases in 1973. At Little Goose Dam the combined transport/control ratio was 15.4:1 for chinook salmon and 13.4:1 for steelhead; the ratios at the hatcheries were 23.5:1 for chinook salmon (Rapid River Hatchery) and 16.4:1 (Dworshak) and 28:1 (Pahsimeroi) for steelhead. One possible reason for the difference might be a differential in benefit which favored hatchery stocks. Because returns to Little Goose Dam were a mixture of hatchery and wild stocks, the proportion of each stock in a sample could alter the transport/control ratio.

Spawning ground surveys for adult chinook salmon were conducted in 1972, 1973, 1975, and 1976. No surveys were made in 1974 because of the small number of marked fish available for recovery. The location of streams surveyed was identical to that described by Ebel et al. (1973). Fourteen marked fish were recovered during the 4 yr of surveys. Of these, 12 were identified as having been released as transports and 2 as controls. Although the recoveries of adults on the spawning grounds were very low, recoveries at Rapid River Hatchery were substantial (Table 14). The fact that 12 adult fish, transported as juveniles from Little Goose Dam, were recovered on the spawning grounds indicates that transported wild stocks as well as hatchery stocks continued their upstream migration after leaving Little Goose Dam.

Straying of Experimental Groups

The chinook spawning grounds of the Okanogan and Methow Rivers and other spring chinook hatcheries in the Columbia River drainage were checked to determine if adult returns from release groups had "strayed" to spawning locations other than their parent stream or hatchery. No strays were indicated in checks of hatcheries and spawning areas in the Columbia River above the mouth of the Snake River, but a few strays (16 chinook salmon and 3 steelhead) were recovered at Pelton Dam on the Deschutes River in Oregon. Of the 16 chinook salmon recovered, 10 were from groups transported as juveniles, 2 from controls, and the remaining 4 could not be positively identified as to release group because tag codes were lost. The three steelhead recovered were also from groups transported. These recoveries indicate that the homing behavior of a portion of the chinook salmon transported as juveniles may have been adversely affected. However, the proportion of the transported groups affected to this degree must have been small; 857 chinook salmon and 2,720 steelhead were identified at Little Goose Dam from the same release groups. The homing behavior of these fish obviously was not damaged. Additional data are needed to quantify the degree of straying that occurs from transporting steelhead and chinook salmon from Little Goose Dam.

DISCUSSION

Comparison of Results With Other Studies

The results of this study are similar to an earlier study done by Ebel et al. (1973) in which survival was definitely increased by transporting the fish downstream as juveniles. Percentage returns of adults to Little Goose Dam from transported fish were greater than that from control fish for the Dalton Point as well as the Bonneville Dam release sites for all 3 yr. However, the estimated percentage returns of chinook salmon were much lower than those reported by Ebel et al. (1973) when fish were collected and transported from Ice Harbor Dam in 1968. Estimated returns of adult chinook salmon, transported as juveniles from Ice Harbor Dam, ranged from 4.3 to 9.0%; whereas, returns of adult chinook salmon, transported as juveniles from Little Goose Dam in this study, ranged from 0.11 to 0.78%—substantially lower than achieved at Ice Harbor Dam.

There are several factors which could have caused the lower percentage returns from Little Goose Dam: 1) some homing ability may have been lost because the fish were intercepted and transported from a location about 130 km farther upstream; 2) the fish collected at Ice Harbor Dam may have been more hardy individuals because they migrated a greater distance, which would have allowed more of the weaker individuals to be eliminated from the populations; 3) the stocks collected at Ice Harbor Dam in 1968 were primarily wild stocks and thus hardier—more able to stand the stress of handling, marking, and hauling; or 4) the general condition of the fish at the time of marking may have been better because the collection, handling, and hauling system used at Ice

Harbor Dam could have resulted in less stress than that at Little Goose Dam. Further examination of the data, however, implies that the condition of the fish (factor 4) may have been the main factor. Estimated adult returns of chinook salmon to Ice Harbor Dam from fish transported in 1969 and 1970 (Slatick et al. 1975) were much lower (0.113-0.581%) than recorded from experimental groups released in 1968. The authors attributed the lower returns to stress caused by the placement of two new dams (Lower Monumental and Little Goose) in the migratory path of the juveniles and from stress caused by the use of a fish pump in the handling operation. The descaling and delayed mortality percentages in the study at Little Goose Dam indicated that stress in the collection, handling, and hauling procedures was a factor.

Steelhead were not affected in the same manner as chinook salmon in either this study or the earlier studies at Ice Harbor Dam. In both studies steelhead returned at a substantially higher rate than chinook salmon. Estimated percentage returns to Little Goose Dam of steelhead that had been transported as juveniles ranged from 1.4 to 2.6%; returns from releases at Ice Harbor Dam in 1969 and 1970 ranged from 0.6 to 1.6%. Since steelhead smolts are larger than chinook salmon smolts, they may have been able to withstand the rigors of collection, handling, and marking; the very low delayed mortality percentages, shown in this study for steelhead, support this reasoning.

Effect of Transportation on Homing

The transport/control ratios provide information on the effect of transportation on homing. For example, if no differential mortality occurred between groups, a steadily decreasing ratio of transport/control numbers from the commercial and sport fisheries below Bonneville Dam to the spawning ground would indicate a loss of homing ability or straying.

During the 3 yr of study, this type of comparison could only be made from 1971 releases of juvenile chinook salmon because the lower river commercial fishery was closed after 1973. A comparison of recovery ratios of adult fish from these releases showed that the transport to control ratios were 2.86, 1.65, and 3.95:1 in the commercial fishery at Little Goose Dam and the spawning grounds,[14] respectively. Although there was a variation in the ratios from the lower river to the spawning grounds, these ratios indicated that ability of transported chinook salmon to home to either their parent stream or Rapid River Hatchery was not seriously damaged by transporting the fish around the seven dams and reservoirs between Little Goose and Bonneville Dams.

The ratios also imply that hatchery stocks were benefited to a greater degree than wild stocks. When returns to the spawning grounds were separated from returns to Rapid River Hatchery and separate transport/control ratios were computed, the ratio for wild stocks became 1.5:1 and hatchery stocks, 4.6:1. However, more data are needed regarding this aspect (only six fish were recovered on the spawning grounds from releases in 1973) before conclusions can be made on the differential effect that transportation might have on hatchery and wild stocks of chinook salmon. A comparison between the ratio in the commercial fishery (2.8:1) and at Little Goose Dam (1.6:1) also indicates that transported chinook salmon may have been affected differently from controls—if one assumes that no differential mortality occurred between control and transported fish as they moved upriver and that wild and hatchery stocks were captured at the same rate in the fishery as they were at Little Goose Dam. Returning adults transported as smolts may have been slightly disoriented or remained for a longer period in the lower river, thus permitting the fishery to take a disproportionate number of transported fish.

Ebel et al. (1973) found no difference in transport/control ratios from the commercial fishery to the spawning grounds when data from releases at Ice Harbor Dam in 1968 were analyzed.

Disproportionate straying of adults from groups transported as juveniles would also be an indication that homing behavior had been affected by the transportation. No straying of either chinook salmon or steelhead was observed in the earlier study at Ice Harbor Dam. On the basis of recoveries of marked chinook salmon in the Deschutes River, some straying of chinook salmon that had been transported as juveniles occurred in this study. This instance of straying and the variations of transport/control ratios from the fishery to Little Goose Dam indicate that the migratory route lost by collecting the juveniles 130 km upstream at Little Goose Dam may be of some importance in determining homing behavior. A current

[14]Return to the hatcheries included in computation of transport/control ratio.

study (Park[15]) being conducted at Lower Granite Dam (about 200 km upstream from Ice Harbor Dam) by NMFS should provide further information on this subject. Preliminary data obtained from adult steelhead and chinook salmon returning to Lower Granite Dam show that transport/control ratios (2.5-2.7:1) obtained from experiments in 1975 and 1976 are similar to those obtained at Little Goose Dam. Insufficient data are available at this writing to determine variations in ratios from the lower river to the estuary or to determine degree of straying.

SUMMARY AND CONCLUSIONS

The main objectives of the research at Little Goose Dam were to determine the effect of transportation on homing and survival of juvenile chinook salmon and steelhead collected at Little Goose Dam and released downstream and to compare these results with an earlier study done at Ice Harbor Dam where fish were transported a shorter distance. The data clearly show that homing ability was not seriously diminished in either chinook salmon or steelhead, and that survival of both species was increased by transporting the fish to release locations downstream from Bonneville Dam.

A comparison of the results of this study with an earlier study done by Ebel et al. (1973) and by Slatick et al. (1975) at Ice Harbor Dam indicates that the effect of collecting the fish about 130 km farther upstream did not seriously diminish their homing ability in comparison with homing ability obtained in the experiment at Ice Harbor Dam. The increases in survival of transported fish noted in the study at Little Goose Dam were also similar to those noted at Ice Harbor Dam, but estimated percentage return of chinook salmon was substantially lower than that achieved at Ice Harbor Dam. Observations made throughout the study indicated that chinook salmon returns might be increased by reducing injury or stress during diversion, collection, and handling process.

The main conclusions bearing on the effect of transporting juveniles from Little Goose Dam to release locations downstream from Bonneville Dam were:

1) Analysis of transport/control ratios obtained from returning adults indicated that returns from naturally migrating juvenile chinook salmon and steelhead that were transported from Little Goose Dam to release locations downstream from Bonneville Dam were increased from 1.1 to 15 times in the fishery and to Little Goose Dam.

2) A significant ($P<0.01$) difference in benefit from transportation was noted between chinook salmon and steelhead; the greatest return and, hence, the greatest benefit occurred with steelhead.

3) Homing of adult fish that had been collected as juveniles at Little Goose Dam and transported several hundred kilometers downstream to Bonneville Dam apparently was not seriously diminished although a small portion ($P<0.02\%$) of the transported adult chinook salmon was known to have strayed.

4) There was no significant ($P<0.05$) difference in adult returns from two release sites tested (Dalton Point and Bonneville Dam) of either steelhead or chinook salmon.

5) Timing of migration of juvenile migrants was not related to timing of adult returns to Little Goose Dam.

6) Neither size nor ocean age of adult steelhead transported experimentally as juveniles was significantly ($P<0.05$) different from controls. Thus transporting the fish did not appear to affect either size or age of returning adult steelhead.

7) Although size of adult chinook salmon transported as juveniles was not significantly ($P<0.05$) different from controls, ocean age was. Transportation, therefore, may have influenced ocean age of returning adult chinook salmon.

ACKNOWLEDGMENTS

I thank Donn Park and Emil Slatick of the Northwest and Alaska Fisheries Center, NMFS, NOAA, for their help in carrying out the operations involved in collecting, marking, and hauling of the thousands of fish involved in this experiment and for their help in compiling the data for analysis. I also wish to thank all of the personnel of the Idaho Department of Fish and Game, Oregon Department of Fish and Wildlife, Washington Department of Fisheries, and the U.S. Fish and Wildlife Service for their cooperation in obtaining adult recoveries. I particularly wish to thank Frank Ossiander, Northwest and Alaska Fisheries Center, NMFS, NOAA, for his advice regarding statistical analysis; Craig MacPhee,

[15]Donn L. Park, Northwest and Alaska Fisheries Center, Natl. Mar. Fish. Serv., NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112, pers. commun. December 1977.

University of Idaho, for his help and advice in preparing this manuscript; and, of course, the U.S. Army Corps of Engineers for their cooperation in providing the facilities and majority of the funding required to do this research. The review of this paper by D. O. Everson, K. E. Hungerford, and R. G. White of the University of Idaho is also appreciated.

LITERATURE CITED

CHANEY, E., AND L. E. PERRY.
1976. Columbia Basin salmon and steelhead analysis summary report, September 1, 1976. Pac. Northwest Reg. Comm., Vancouver, Wash., 74 p.

EBEL, W. J.
1974. Marking fishes and invertebrates. III. Coded wire tags useful in automatic recovery of chinook salmon and steelhead trout. Mar. Fish. Rev. 36(7):10-13.

EBEL, W. J., D. L. PARK, AND R. C. JOHNSEN.
1973. Effects of transportation on survival and homing of Snake River chinook salmon and steelhead trout. Fish. Bull., U.S. 71:549-563.

EBEL, W. J., AND H. L. RAYMOND.
1976. Effect of atmospheric gas supersaturation on salmon and steelhead trout of the Snake and Columbia Rivers. Mar. Fish. Rev. 38(7):1-14.

ELLIS, C. H., AND R. E. NOBLE.
[1961.] Barging and hauling experiments with fall chinook salmon on the Klickitat River to test effects on survivals. 1960 Annu. Rep. Wash. Dep. Fish., p. 57-71.

GROVES, A. B., G. B. COLLINS, AND P. S. TREFETHEN.
1968. Roles of olfaction and vision in choice of spawning site by homing adult chinook salmon (*Oncorhynchus tshawytscha*). J. Fish. Res. Board Can. 25:867-876.

HASLER, A. D., AND W. J. WISBY.
1951. Discrimination of stream odors by fishes and its relation to parent stream behavior. Am. Nat. 85:223-238.

JEFFERTS, K. B., P. K. BERGMAN, AND H. F. FISCUS.
1963. A coded wire identification system for macroorganisms. Nature (Lond.) 198:460-462.

KOO, T. S. Y.
1962. Age designation in salmon. *In* T. S. Y. Koo (editor), Studies of Alaska red salmon, p. 37-48. Univ. Wash. Publ. Fish., New Ser. 1.

PARK, D. L., AND W. J. EBEL.
1974. Marking fishes and invertebrates. II. Brand size and configuration in relation to long-term retention on steelhead trout and chinook salmon. Mar. Fish. Rev. 36(7):7-9.

RAYMOND, H. L.
1968. Migration rates of yearling chinook salmon in relation to flows and impoundments in the Columbia and Snake Rivers. Trans. Am. Fish. Soc. 97:356-359.
1969. Effect of John Day Reservoir on the migration rate of juvenile chinook salmon in the Columbia River. Trans. Am. Fish. Soc. 98:513-514.
1979. Effects of dams and impoundments on migrations of juvenile chinook salmon and steelhead from the Snake River, 1966 to 1975. Trans. Am. Fish. Soc. 108:505-529.

SCHOLZ, A. T., J. C. COOPER, D. M. MADISON, R. M. HORRALL, A. D. HASLER, A. E. DIZON, AND R. J. POFF.
1973. Olfactory imprinting in coho salmon: behavioral and electrophysiological evidence. Proc. 16 Conf. Great Lakes Res., p. 143-153.

SHAPIRO, S. S., AND M. B. WILK.
1965. An analysis of variance test for normality (complete samples). Biometrika 52:591-611.

SLATICK, E.
1976. Comparative retention of dart and jaw tags on chinook salmon and steelhead trout during their spawning migration. Mar. Fish. Rev. 38(7):24-26.

SLATICK, E., D. L. PARK, AND W. J. EBEL.
1975. Further studies regarding effects of transportation on survival and homing of Snake River chinook salmon and steelhead trout. Fish. Bull., U.S. 73:925-931.

SMITH, J. R., AND W. J. EBEL.
1973. Aircraft-refueling trailer modified to haul salmon and trout. Mar. Fish. Rev. 35(8):37-40.

SMITH, J. R., AND W. E. FARR.
1975. Bypass and collection system for protection of juvenile salmon and trout at Little Goose Dam. Mar. Fish. Rev. 37(2):31-35.

SNYDER, J. O.
1928. Salmon investigations. Calif. Fish. Game 14: 25-29.

IS OVULATION IN DOLPHINS, *STENELLA LONGIROSTRIS* AND *STENELLA ATTENUATA*, ALWAYS COPULATION-INDUCED?

K. Benirschke,[1, 2] Mary L. Johnson,[2] and Rolf J. Benirschke[3]

ABSTRACT

This study of 58 nonpregnant uteri and ovaries of the spinner dolphin, *Stenella longirostris*, and the spotted dolphin, S. attenuata, was undertaken to ascertain whether ovulation is copulation-induced (reflex) or occurs spontaneously. Control specimens of immature, pregnant, and lactating females were examined also and were used to define the normal reproductive events in uteri and ovaries of these species. No differences were found between the two species. In about one half of the specimens we found active corpora lutea of recent origin and in another 15% of *S. attenuata* and 29% of *S. longirostris*, corpora had fibrous centers but were hormonally active. No embryos were found and the endometrial changes were such that early but unobserved pregnancies could be excluded. In 35% of the specimens from *S. attenuata* the macroscopic diagnosis of corpus luteum was erroneous, while this was true of 21% in *S. longirostris*. The corpora were degenerating and more resembled early corpora albicantia histologically. In two of these specimens, endometritis was found and the endometrial histology gave evidence of abortion in three. These findings are evidence that these *Stenella* species may sometimes ovulate spontaneously and that macroscopic classification of corpora lutea in the past may frequently have been erroneous.

The reproductive physiology of the spotted dolphin, *Stenella attenuata*, and spinner dolphin, *S. longirostris*, has not been fully elucidated. In particular, it is presently unknown whether these dolphins ovulate spontaneously or on reflex after copulation. Some reasons to believe the latter have been presented for *Tursiops truncatus* (Harrison 1977) and the same is implied for other Cetacea. The finding of corpora lutea almost exclusively in pregnant animals is the basis for this assumption, and the purpose of this study is to examine the genital tracts of 58 nonpregnant animals with corpora lutea in detail in an attempt to resolve this question. In a detailed study of spotted dolphin, Perrin et al. (1976) found that of 242 females with corpora lutea, 229 (95%) were pregnant. In a similar study of spinner dolphins, Perrin et al. (1977) found that 2.8% of 536 adult females contained corpora lutea whose presence could not be explained by pregnancy, lactation, or abortion.

The distribution of species with and without reflex ovulation has been reviewed by Jöchle (1973). A surprisingly large number of species is listed as having exclusively or predominantly reflex ovulation, including Cetacea. Only primates, mouse and rat are cited as exceptions; however, modern studies suggest this to be an incomplete list. In several papers on Camelidae, reflex ovulation is well supported by experimental studies and by observations from abatoirs. Although camels and their South American relatives must be accepted as being reflex ovulators, the carefully controlled study by England et al. (1969) showed that "occasional spontaneous ovulation occurred during the height of the breeding season" in the llama, *Lama glama*.

In an attempt to gain additional information on the reproductive physiology of *S. longirostris* and *S. attenuata*, we examined the reproductive tracts of animals recorded to possess corpora lutea while not pregnant. Special attention was paid to ascertaining any reasons for the existence of these corpora lutea, such as early undetected pregnancy and an attempt was made to correlate the ovarian status with endometrial changes.

MATERIALS AND METHODS

Reproductive tracts of female *S. longirostris* and *S. attenuata* were collected at sea by observers during commercial tuna fishing operations in the southeastern Pacific Ocean (Perrin et al. 1976,

[1]Research Department, San Diego Zoo, P.O. Box 551, San Diego, CA 92112.
[2]University of California, San Diego, La Jolla, CA 92093.
[3]San Diego Chargers, P.O. Box 20666, San Diego, CA 92121.

Manuscript accepted October 1979.
FISHERY BULLETIN: VOL. 78, NO. 2, 1980.

1977). The organs were preserved in 10% Formalin[4] (Mallinkrodt) solution and stored at the Southwest Fisheries Center (SWFC), National Marine Fisheries Service, NOAA, La Jolla, Calif. At the time of capture, a variety of observations were recorded, including identified pregnancy, size of the fetus, and lactation. These data, dates and location of capture as well as related pertinent information, are recorded in logs at SWFC. Here also the ovaries were sliced at 1 mm intervals, and observations such as the presence of corpora lutea, corpora albicantia, and ovarian size were recorded and correlated with capture information. Those apparently gravid uteri whose ovaries had a corpus luteum were dissected further and, occasionally, small fetuses were identified by SWFC staff. In addition, the present authors carefully dissected three intact uteri of the 1977 catches where ovaries contained corpora lutea but in which pregnancy had not been recorded.

For the purpose of the present study the reproductive tracts of 53 nonpregnant dolphins, captured in 1976, and whose ovaries were recorded to contain corpora lutea, were examined in detail. A few specimens of 1975 and 1977 were also studied and are included, bringing the figure to 58 genital tracts. The tabulation of the reproductive condition of these tracts is shown in Table 1.

These specimens represent the majority of reproductive tracts recorded to possess unexplained corpora lutea in 1976. There were 67 in all but not all of the specimens were in suitable condition for inclusion in this study. Thus, several were too severely autolyzed for proper evaluation; in others, either the complete ovaries or uteri could not be located in the specimen collection.

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Reproductive tracts of *Stenella* spp. studied because corpora lutea were found in the absence of pregnancy or lactation.

Species	1975	1976	1977
Stenella longirostris	0	38	0
S. attenuata	2	15	3

In an effort to better understand the macroscopic and histologic features of dolphins with known reproductive events, it was desirable to select suitable control material from the same stored collection. Six groups of specimens were selected for this purpose and consisted of the following specimens: Group I, 3 tracts of immature *S. longirostris*; Group II, 6 tracts of mature female *S. longirostris* having no corpus luteum and, therefore, termed "resting"; Group III, 12 tracts of *S. longirostris* with early pregnancy, the embryos measuring from 1 to 53 mm long (1-5 g with placenta); Group IV, 6 tracts of later pregnant dolphins (4 *S. longirostris* and 2 *S. attenuata*) with fetal sizes ranging from 300 to 725 mm; Group V, 11 tracts of lactating, nonpregnant females (10 *S. longirostris* and 1 *S. attenuata*); Group VI, the experimental group, 58 tracts of nonpregnant females possessing a corpus luteum (38 *S. longirostris* and 20 *S. attenuata*; Table 1); for a total of 96 female genital tracts.

The gross examination of genital tracts by us ascertained the following standard information: Weight; length and width of uterine horns and cervices; thickness of uterine walls at standard locations. Histologic sections, stained with hematoxylin and eosin, were prepared from standard locations of tubes, uterine horns, lower uterine segments, and ovaries (Figure 1). Measurements of uterine mucosa and muscularis were made at low power microscopic examination with the aid of a calibrated ocular micrometer. At histologic examination the uterine findings (glands, secretion, mitoses, edema, hyalinization, inflammation) were compared with the ovarian activity. Relevant photomicrographs were made with a Zeiss Axiomat.

RESULTS

Controls

Group I, Immature Females

These three *S. longirostris* measured from 164 to 176 cm body length (Table 2) and possessed neither

TABLE 2.—Group I: Immature controls, *Stenella longirostris* captured on 20 February 1976.

Specimen no.	Dolphin length (cm)	Uterus weight (g)	Left horn of uterus				Right horn of uterus			
			Length (cm)	Endometrial fold (mm)	Endometrial valley (mm)	Myometrium (mm)	Length (cm)	Endometrial fold (mm)	Endometrial valley (mm)	Myometrium (mm)
1	176	47	10	1.49	0.60	0.54	9	2.09	0.75	0.60
2	168	44	9	1.34	0.39	0.60	9	1.07	0.36	0.62
3	164	22	9	1.10	0.60	0.42	7	1.07	0.36	0.54
			Average	1.31	0.53	0.52		1.41	0.59	0.58

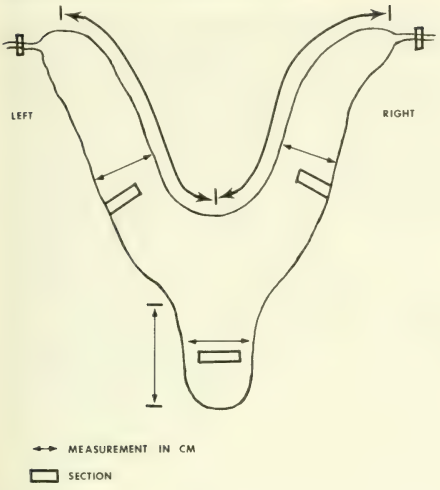


FIGURE 1.—Diagram of dolphin uterus. Arrows indicate measurements taken in *Stenella* spp. and squares denote location of histologic sections.

corpora lutea nor corpora albicantia. Because of their size it was assumed that they were at the verge of maturity. As shown in Figure 2, uterine horns were of equal size, there were no stretch marks and the endometrium was flat. Numerous Graafian follicles of varying stages of development were present in both ovaries, but there was no evidence of ovulation. The endometrium was thin and composed of tubular glands possessing neither secretion nor mitoses; the stroma was devoid of inflammation and edema or hyalinization (Figure 3). The fallopian tubes were small and empty. In all subsequent specimens, slides of fallopian tubes were examined. No relevant changes were observed and they are therefore not described further. Also, sections of the lower uterine segment were found to make no contribution in the assessment of reproductive state and are not included in this analysis.

Group II, Mature Females

These six *S. longirostris* measured from 173 to 186 cm in length and were adjudged to be mature

FIGURE 2.—Immature uterus of *Stenella longirostris* (no. 1, Table 2). Note the flat folds of endometrium, equal-sized horns, and lack of serosal stretch marks (center)

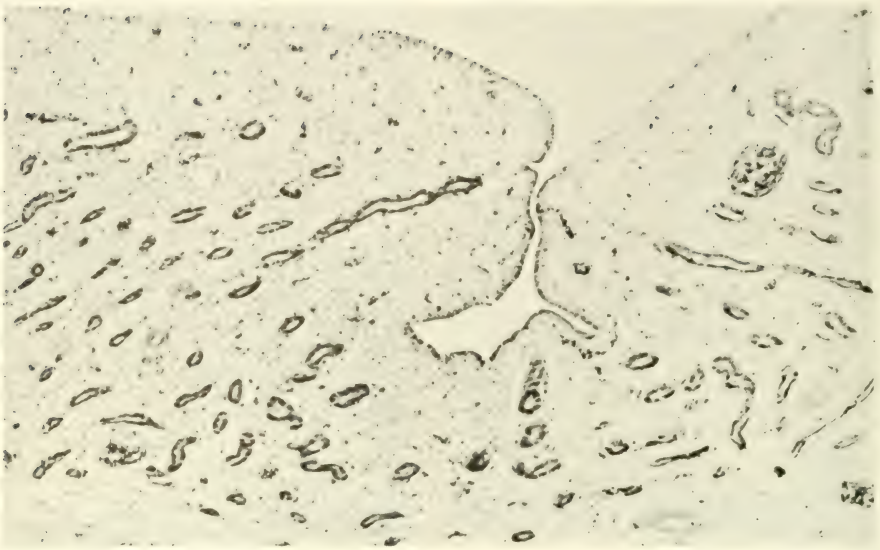


FIGURE 3.—Endometrium of immature *Stenella longirostris* (no. 3, Table 2). Tubular glands, little folding, thin endometrium, no secretion or mitoses (hematoxylin and eosin × 60).

because of their size and the presence of at least one corpus albicans. They were not lactating nor did they possess a corpus luteum. The appropriate measurements are set forth in Table 3. In general, the horns were asymmetrical but not so markedly as those of lactating females (Group V), with the exception of specimen no. 4 (Table 3). The wrinkled serosa and congestion of endometrium of this animal's left horn indicated recent pregnancy (Figure 4). All but one female of this group had "stretch marks" which we assumed to be an indication of previous pregnancy. Microscopic study of the corpora albicantia in this group allowed some correlation with the endometrial findings. Thus, the apparently most recently delivered uterus (Figure 4) had a still cellular corpus albicans (Figure 5) and, inflammatory cells, hemosiderin macrophages and stromal hyalinization were observed in the congested endometrium (Figure 6). In the others, judged to have had past pregnancies, the corpus albicans was less cellular, more hyalinized and shrunken. The endometrium did not appear to be stimulated, had thin epithelium, no mitoses but scattered macrophages were in the process of removing debris. Apparently later still, Graafian follicle development commences, uterine horns are of nearly equal size and endometrial glandular redevelopment occurs with mitoses, glandular convolutions, occasional epithelial vacuoles, and stromal edema (Figure 7).

TABLE 3.—Group II: Mature controls, *Stenella longirostris*, for 1976.

Specimen no.	Month of capture	Dolphin length (cm)	Uterus weight (g)	Left horn of uterus				Right horn of uterus			
				Length (cm)	Endometrial fold (mm)	Endometrial valley (mm)	Myometrium (mm)	Length (cm)	Endometrial fold (mm)	Endometrial valley (mm)	Myometrium (mm)
1	February	186	108	13	1.79	0.75	1.49	10	1.94	0.66	1.49
2	February	181	123	17	2.70	0.75	1.04	15	2.24	0.90	0.90
3	February	179	136	13	1.79	0.66	1.19	11	1.19	0.75	1.64
4	February	178	152	17	2.99	0.90	2.39	8	4.78	0.90	1.94
5	July	175	98	16	1.64	0.30	0.90	18	1.49	0.60	1.49
6	June	173	110	23	4.18	0.90	1.49	18	3.58	1.04	1.49
				Average	2.52	0.71	1.42		2.54	0.81	1.49

FIGURE 4.—Mature animal's uterus, presumably recently delivered (no. 4, Table 3). Note larger left horn with congestion and serosal stretch marks.

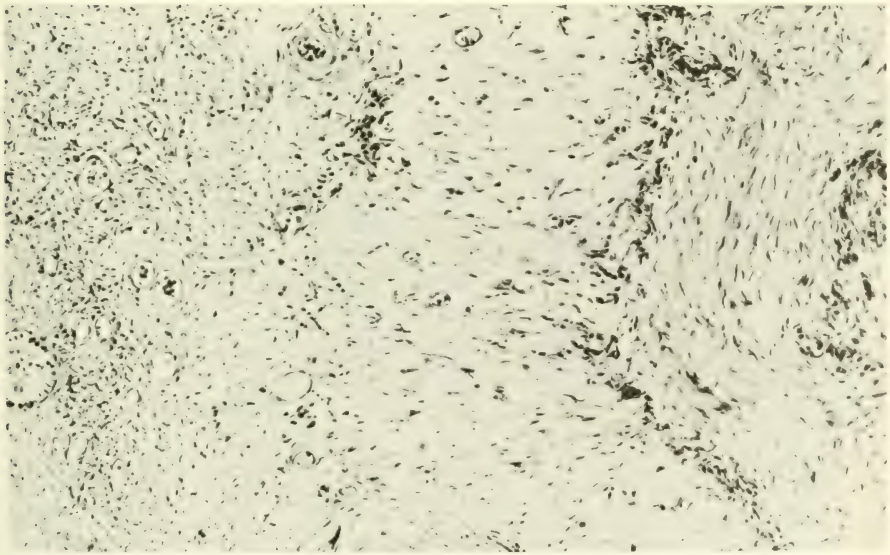


FIGURE 5.—Corpus albicans of animal in Figure 4. At right is former follicular cavity, replaced by young fibroblastic tissue. Dark cells in central (former luteal) band of corpus albicans suggest recent conversion of corpus luteum to corpus albicans (hematoxylin and eosin × 120).

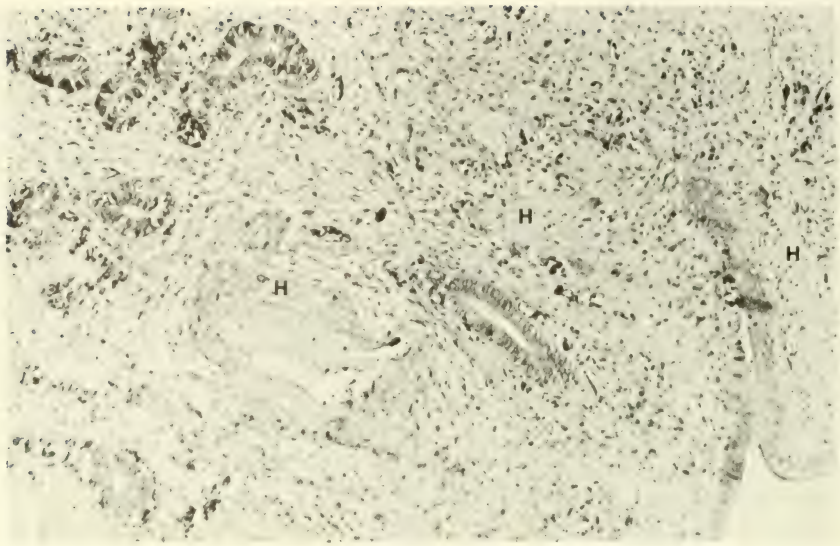


FIGURE 6.—Endometrium of animal in Figures 4 and 5, surface at right. Infiltration of stroma with macrophages; sparse glands; hyalinization of stroma and larger vessel walls at H (hematoxylin and eosin × 120).

Group III, Early Pregnancy

There were 12 *S. longirostris* in this group measuring from 166 to 188 cm in length (Table 4). With the exception of the first specimen listed, the left uterine horn was the larger. In this exceptional animal, the corpus luteum was also on the right and no corpus albicans was found in the left side. Uterine size and weight did not correlate well with embryonic size (1-53 mm) or weight (1-5 g). The embryos had been removed previously and their placentas had apparently not yet implanted. The larger (pregnant) horn had a congested endometrium and distended lumen (Figure 8).

This is an important control group for the experimental Group VI whose uteri were empty despite the presence of a corpus luteum. Thus, it is noteworthy that even in small embryos (Figure 9) the placental membranes are of appreciable size and they grow rapidly (Figure 10) so that they are not easily overlooked in dissections. Early limb bud development could be recognized in embryos sized 5 mm or more.

TABLE 4.—Group III: Early pregnant controls, *Stenella longirostris*. All from February 1976 except no. 11 captured in May 1976.

Specimen no.	Dolphin length (cm)	Uterus weight (g)	Left horn of uterus				Right horn of uterus				Fetus	
			Length (cm)	Endometrial fold (mm)	Endometrial valley (mm)	Myometrium (mm)	Length (cm)	Endometrial fold (mm)	Endometrial valley (mm)	Myometrium (mm)	Length (mm)	Weight (g)
1	176	140	10	6.87	1.49	1.49	15	5.37	1.49	1.49	1	1
2	172	171	20	—	—	—	12	5.67	1.19	1.49	2	1
3	178	145	15	5.07	0.90	1.49	12	4.03	1.04	1.94	2	1
4	181	208	28	2.69	1.19	0.96	20	2.69	0.90	0.78	5	1
5	188	163	20	2.83	0.75	0.04	15	2.99	0.75	1.04	5	2
6	172	192	19	5.97	1.19	1.04	12	6.87	1.79	1.49	5	2
7	166	204	17	6.87	0.75	0.90	11	7.46	1.34	0.75	5	2
8	176	212	25	5.37	1.49	1.04	15	3.88	0.60	1.19	5	2
9	167	227	19	6.87	1.19	1.94	13	—	2.39	1.49	5	2
10	184	229	28	2.09	0.36	1.04	15	3.58	0.90	1.19	5	2
11	180	144	17	4.78	1.19	1.04	13	2.99	1.19	1.19	8	2
12	180	187	23	1.04	0.35	0.90	16	2.09	0.30	0.90	53	5
			Average	4.68	0.99	1.17		4.33	1.16	1.25		

FIGURE 7.—Endometrium undergoing early stimulation, presumably after past pregnancy (no. 3, Table 3). Glands are more numerous and coiled. They contain occasional epithelial secretory vacuoles and mitoses. Focal edema (E) of stroma commences (hematoxylin and eosin × 60).

FIGURE 8.—Early pregnant uterus with distended left horn and hyperemia of endometrium (no. 4, Table 4).

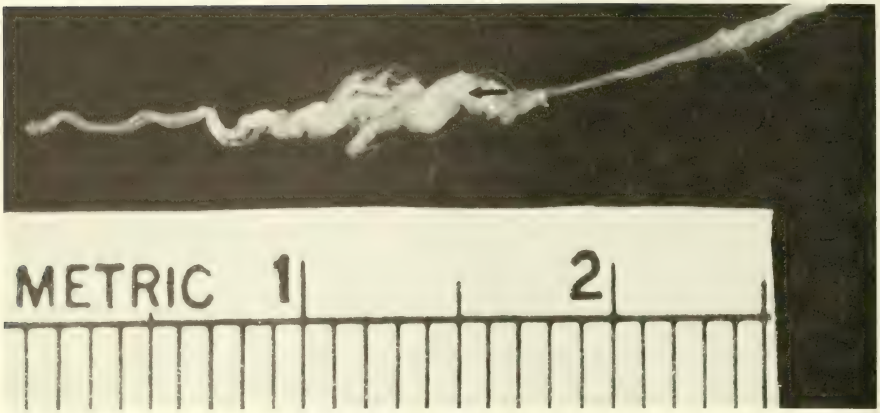


FIGURE 9.—Smallest (2 mm) normal embryo at arrow with long, filmy placental membranes (no. 3, Table 4).

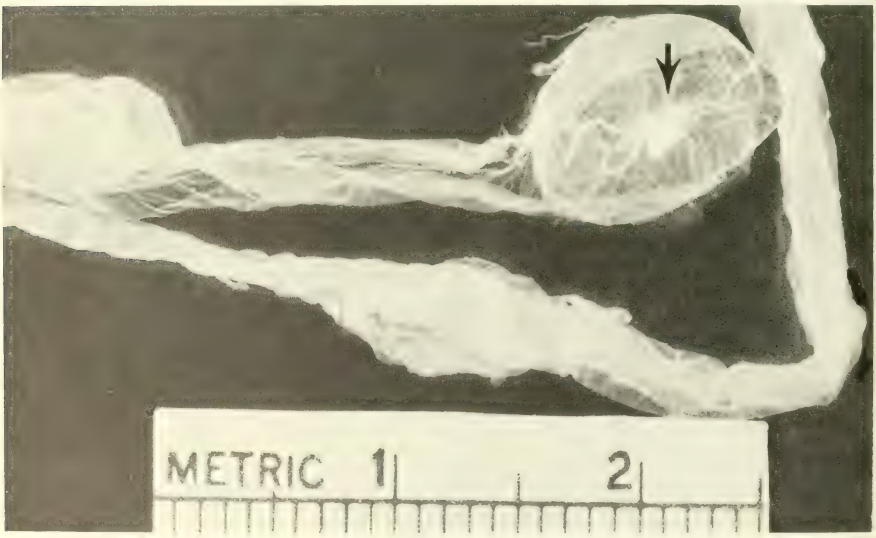


FIGURE 10.—Five mm embryo (arrow) with huge placental membranes (no. 9, Table 4).

The cells of the corpus luteum of all of these animals were well supported, and the central fibrin clot was invaded by vessels and fibroblasts in all but one animal (no. 3, Table 4; Figure 9). This was also the smallest embryo other than that of the aberrant right specimen (no. 1, Table 4). Its corpus luteum is shown in Figure 11 and is readily distinguishable from the small luteal mass found in the experimental group.

The endometrium had characteristic changes that should allow the histologic diagnosis of early pregnancy. First, the tips of endometrial folds be-

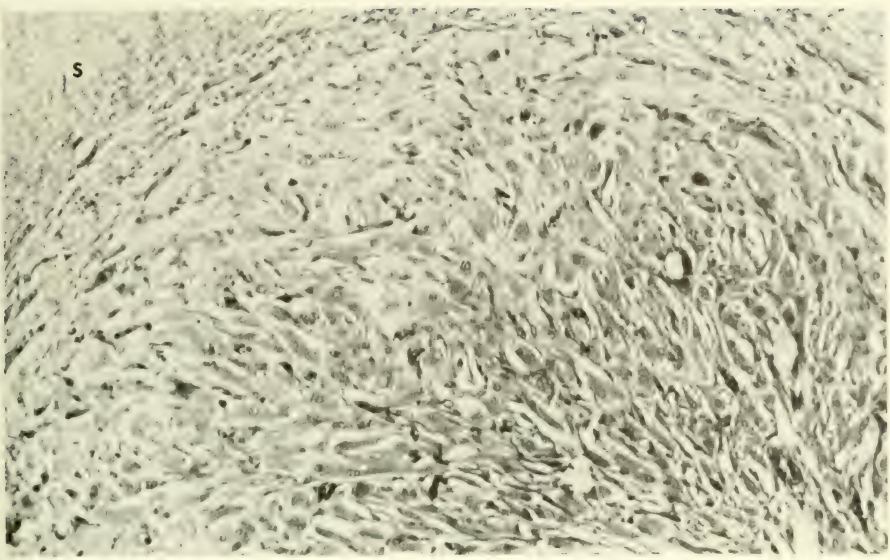


FIGURE 11.—Portion of active corpus luteum of earliest pregnancy with cavity at bottom right and ovarian stroma (S) at top left (no. 3, Table 4; hematoxylin and eosin × 100).

come edematous (Figure 12). At this stage the glands are empty and crowded in the basal portions. Their epithelium lacked mitoses. With advancing pregnancy the edema diminished while secretion accumulated in glands. Most characteristic, however, is the development of a rich capillary network with congestion, most notably in the superficial strata (Figure 13). Despite the presence of significant chronic endometritis in two cases, normally developing early embryos were found.

Group IV, Late Pregnancy

We selected four *S. longirostris* and two *S. attenuata* between 165 and 199 cm in length and embryos of 300-725 mm in length (the *S. attenuata* fetuses were lost at sea) for this comparison (Table 5). All implantations were in the larger left horn but a portion of the membranes traversed into the right horn. The large single corpus luteum of these six specimens was present in the left ovary.

The superficial endometrium was extremely arborized with distended glands into which the villi of the epitheliochorial placenta penetrated, forming an intimately interdigitating connection (Figure 14). The basal endometrium was edematous and glands contained secretion. With advancing gestation the villous arborization increased. The corpus luteum had characteristic appearance (Figure 15). Among the plump, eosinophilic luteal cells streamers of fibrocytes gave the first appear-

TABLE 5.—Group IV: Late pregnant controls. Specimen no. 1-4 *Stenella longirostris*, captured October 1978; no. 5-6 *S. attenuata*, captured July 1976.

Specimen no.	Dolphin length (cm)	Weight of placenta and uterus (g)	Left uterine horn				Right uterine horn				Fetus length (mm)
			Length (cm)	Endometrial fold (mm)	Endometrial valley (mm)	Myometrium (mm)	Length (cm)	Endometrial fold (mm)	Endometrial valley (mm)	Myometrium (mm)	
1	197	617	—	—	—	0.60	—	—	—	0.75	300
2	182	703	42	—	—	—	21	—	—	—	429
3	165	700	60	2.69	0.60	0.75	26	5.97	1.49	1.19	557
4	168	982	64	1.79	0.60	0.60	20	—	—	—	725
5	—	730	—	—	—	1.79	12	—	—	0.75	—
6	—	965	—	—	—	2.08	21	—	—	0.60	—

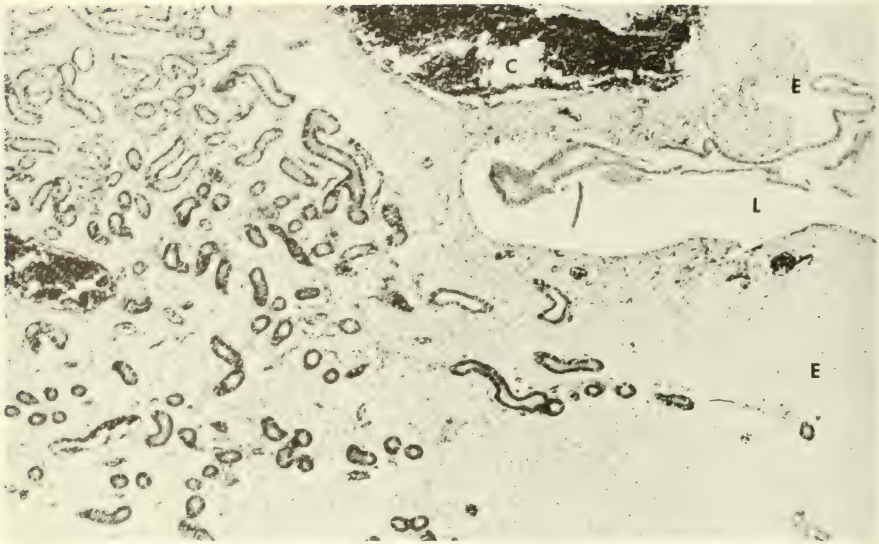


FIGURE 12.—Endometrium of earliest pregnancy (Figures 9, 11; no. 3, Table 4). Uterine lumen (L) at right. Note the marked edema (E) in superficial stroma, congestion (C) and compact arrangement of secretory glands at left (hematoxylin and eosin × 50).

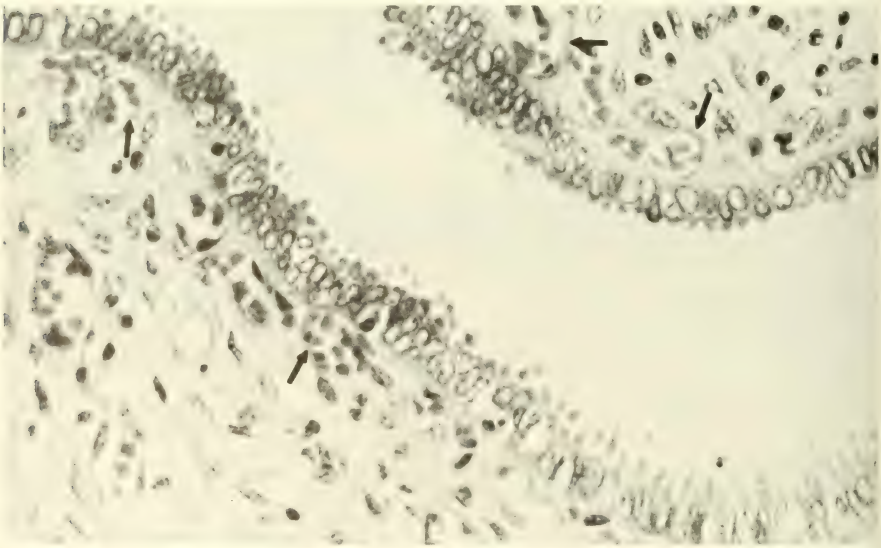


FIGURE 13.—Typical capillary distension (arrows) and neovascularization of endometrial stroma immediately beneath surface endometrial epithelium in early pregnancy (no. 9, Table 4; hematoxylin and eosin × 300).

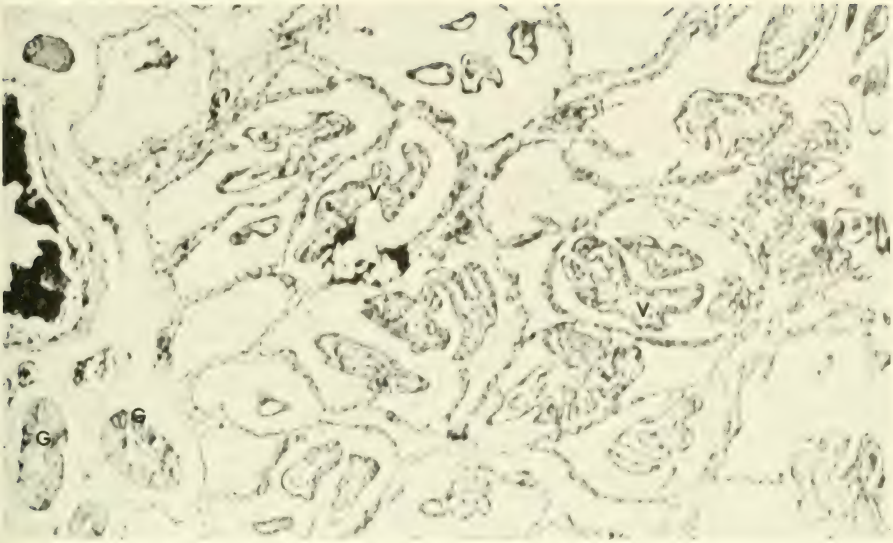


FIGURE 14.—Placental attachment with basal endometrial glands (G) at left and interdigitating villi (V) within distended glandular lumina (no. 2, Table 5; hematoxylin and eosin × 80).

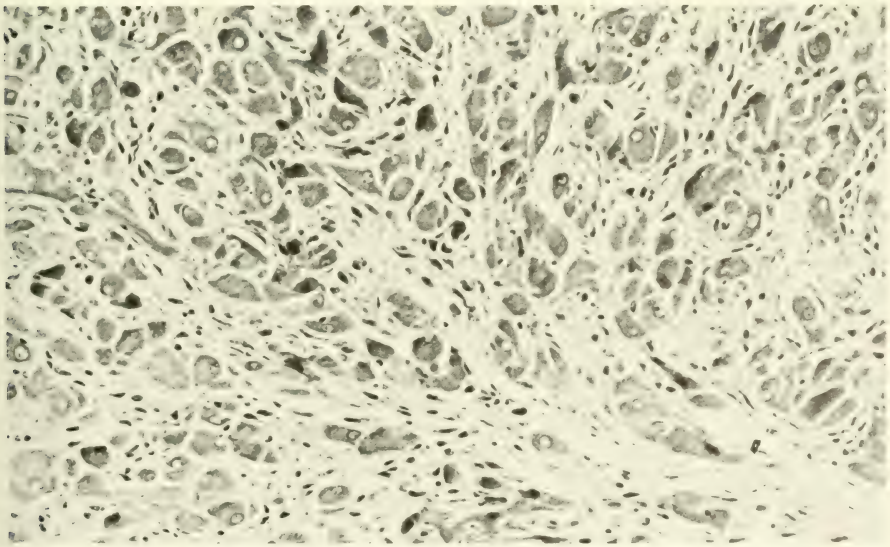


FIGURE 15.—Corpus luteum of uterus shown in Figure 14, the organized cavity is at bottom right. Note well-supported dark luteal cells with fibrocytes in between (hematoxylin and eosin × 150).

ance of degeneration. This connective tissue became less apparent with advancing pregnancy.

Group V, Lactating Females

Six specimens were selected measuring from 167 to 182 cm (*S. longirostris*) and one 202 cm (*S. attenuata*). They had been identified as lactating during dissection at sea. It is a heterogeneous group as judged by uterine size, endometrial histology, and the appearance of the corpora albicantia (Table 6). Some animals must have delivered very recently as evidenced by the marked disparity of uterine horn size, hyperemia, and the recent degenerative changes in the corpus luteum, while others had more equal horns and well-advanced corpora albicantia. No active corpora lutea were present while at least one corpus albicans was found in all specimens. Some corpora albicantia had chronic inflammatory cell infiltration and four ovaries had Graafian follicles maturing at various stages. Stretch marks were present on the uterine serosa and the endometrium had typical involutional changes histologically. Beneath the surface epithelium there was a thin zone of hyalinization in most specimens, while recently delivered animals had prominent, congested vessels in myometrium and endometrium. Some of these had hyalinized walls also. In a majority of endometria a mild chronic inflammatory infiltrate was present; one had acute pyometritis. No mitoses or edema was present, the endometria appeared "resting." Hemosiderin-laden macrophages in endometrium or lower uterine segment were present in three, presumably due to interstitial hemorrhage at recent delivery. Such deposits were found in only one other female (Control Group II) whom we suspect to have delivered recently but who was not recorded as lactating.

Experimental Groups

Group VI, Nonpregnant Animals With Corpus Luteum

The 58 animals of this group were not detected to be pregnant at sea but had a corpus luteum present in one of their ovaries. The group is divided into three subgroups made up of specimens with corpora lutea at different stages of development or involution.

GROUP VIa.—These 28 animals (19 *S. longirostris*; 9 *S. attenuata*) measured 163-191 cm in length, and the group was of special importance because the corpora lutea were judged to be the youngest. For this reason, an early pregnancy could have been overlooked. Two intact uteri were dissected meticulously, including the fallopian tubes. Neither embryos nor placentas were identified in any of the 28 specimens. From the dates of capture (Table 7) it will be noted that most (17) were captured in February, as is also true of early pregnant animals (Table 4). These figures must be interpreted with caution, however, because of different catch sizes on various cruises. The macroscopic findings were not uniform in that uterine weight varied between 90 and 467 g, the horn sizes varied considerably and endometrium was as often congested or mucus-covered as not. Only once was the corpus luteum found in the right ovary.

The histologic appearance of the endometrium correlated neatly with the corpus luteum development and grouping was undertaken accordingly. Those specimens whose corpus luteum had a central fibrin-filled cavity were placed into Group VIa; those whose cavity was replaced by fibrous tissue were adjudged to have ovulated earlier and

TABLE 6.—Group V: Lactating controls. Specimen no. 1-10 *Stenella longirostris*; no. 11 *S. attenuata*.

Specimen no.	Month and year of capture	Dolphin length (cm)	Uterus weight (g)	Left uterine horn				Right uterine horn				Graafian follicle	Corpus albicans
				Length (cm)	Endometrial fold (mm)	Endometrial valley (mm)	Myometrium (mm)	Length (cm)	Endometrial fold (mm)	Endometrial valley (mm)	Myometrium (mm)		
1	Feb. 1976	171	113	14	2.24	0.21	1.64	8	—	0.60	0.90	no	+
2	Feb. 1976	182	112	13	2.29	0.57	2.54	9	2.99	0.66	1.04	+	+
3	Feb. 1976	171	73	11	1.73	0.24	1.64	9	1.19	0.39	1.94	+	+
4	June 1976	171	65	12	1.34	0.30	2.99	11	1.79	0.30	2.09	no	+
5	June 1976	167	126	20	3.88	0.60	1.04	13	3.58	1.64	1.34	+	+
6	Feb. 1976	174	74	15	1.79	0.60	1.49	8	2.24	0.75	0.90	no	+
7	Feb. 1976	175	109	17	2.99	0.24	1.79	8	2.99	0.66	0.90	no	+
8	Feb. 1976	174	198	21	7.91	0.90	2.09	13	6.87	1.13	1.19	no	+
9	Feb. 1976	173	112	12	4.78	1.04	1.04	10	2.09	0.45	1.06	no	+
10	June 1976	173	60	13	1.49	0.75	2.09	12	1.19	0.60	0.75	+	+
11	Sept. 1977	202	550	—	1.64	0.75	2.09	—	1.64	0.60	1.34	no	+
		S. longirostris — Average		3.04	0.56	1.84			2.77	0.72	1.21		

TABLE 7.—Group VIa: Experimental group with early corpora lutea. Specimen no. 1-19 *Stenella longirostris*; no. 20-28 *S. attenuata*.

Specimen no.	Month and year of capture	Dolphin length (cm)	Uterus weight (g)	Left horn of uterus				Right horn of uterus			
				Length (cm)	Endometrial fold (mm)	Endometrial valley (mm)	Myometrium (mm)	Length (cm)	Endometrial fold (mm)	Endometrial valley (mm)	Myometrium (mm)
1	Feb. 1976	184	120	15	5.37	1.72	1.04	19	2.69	1.04	0.75
2	Apr. 1976	182	132	14	4.78	1.49	0.60	14	5.67	1.19	0.75
3	Feb. 1976	171	—	26	4.18	1.49	1.34	16	4.48	1.34	0.60
4	Feb. 1976	176	—	16	4.48	1.94	1.49	14	4.02	1.49	1.34
5	Feb. 1976	173	—	16	2.84	1.19	0.45	18	—	—	0.75
6	Feb. 1976	149	90	15	3.13	0.90	0.96	15	4.18	1.19	1.04
7	Feb. 1976	180	119	25	6.56	0.75	1.34	13	4.18	1.04	1.04
8	Feb. 1976	180	166	20	2.53	0.75	1.04	14	4.18	1.79	0.90
9	Feb. 1976	184	217	25	4.48	1.49	1.19	20	3.28	1.40	0.90
10	Feb. 1976	183	224	18	8.66	1.19	1.34	15	5.97	0.75	1.04
11	Feb. 1976	181	167	16	4.48	1.19	1.94	14	5.97	1.04	0.90
12	Feb. 1976	188	180	18	8.35	0.60	1.79	12	4.78	1.19	0.90
13	Aug. 1976	163	127	16	8.96	0.90	0.90	12	4.48	1.49	1.19
14	Feb. 1976	168	158	21	3.58	1.19	2.69	13	5.07	1.79	1.64
15	Feb. 1976	177	118	20	3.13	0.90	1.49	14	4.18	0.60	0.96
16	Feb. 1976	167	111	17	3.28	2.09	1.04	15	3.58	1.79	0.75
17	Feb. 1976	176	—	22	4.78	0.96	1.34	14	3.58	0.75	1.04
18	Feb. 1976	171	—	14	4.18	1.64	1.19	11	3.28	1.49	1.04
19	Aug. 1976	167	165	22	5.97	2.99	1.49	21	3.88	1.64	0.90
			S. longirostris — Average		4.93	1.33	1.29		4.30	1.28	0.77
20	Oct. 1976	174	190	29	3.88	0.60	1.49	18	3.28	0.84	2.09
21	Feb. 1976	189	192	23	2.98	0.60	1.49	19	2.38	1.19	1.49
22	Aug. 1976	176	390	35	7.46	1.49	1.64	15	—	1.19	1.49
23	Oct. 1975	191	156	25	4.93	1.04	1.34	14	3.58	1.04	1.34
24	Aug. 1976	174	333	26	7.16	1.79	1.94	16	2.99	0.75	1.19
25	May 1976	185	467	27	6.57	1.19	2.39	17	4.48	0.90	1.64
26	Apr. 1976	180	154	18	4.18	1.19	0.90	20	3.28	1.79	1.04
27	June 1977	185	190	12	2.69	0.90	1.19	17	1.79	0.30	0.75
28	June 1977	186	220	13	2.84	0.90	0.90	12	2.39	0.45	1.49
			S. attenuata — Average		4.74	1.01	1.48		3.02	0.94	1.39

placed into Group VIb. Because of the potential insight these specimens give into the dynamics of ovarian/endometrial relationships, these specimens are described in more detail.

When the Graafian follicle has recently ruptured, stromal vessels infiltrate the granulosa layer (Figure 16). The follicular lumen is filled with serous fluid and fibrin but rarely contains blood as in many other species. The corresponding endometrial stroma is edematous, the glands are tubular, lack secretory vacuoles and contain mitoses (Figure 17). When the corpus luteum is better established, the central cavity is more pronounced, capillaries have penetrated the granulosa layer, and, in contrast to its cells in specimens from early pregnancy (Figure 11), they possess less cytoplasm, being less plump (Figure 18). It should again be noted that the cavities rarely contain red blood cells. The endometrial glands at this stage are more crowded, have more coiling, and still possess mitoses, but the earliest appearance of epithelial cytoplasmic vacuoles occurs (Figure 19). The vacuolization appears to commence under the endometrial surface and penetrates slowly throughout the entire thickness of the endometrium (Figure 20). At the same time, fibroblastic infiltration of the corpus luteum cavity has taken place and the luteinized cell wall has folded remarkably. Very few mitoses were found in superficial endometrial cells at this stage and in the final stages before the central corpus luteum cavity has been completely filled in by fibrous tissue, the endometrial stromal edema disappears, to be replaced by coiled secretory glands (Figure 21). No mitoses exist, nor is secretion exuded into the glandular lumina. Such corpora lutea are expected to be associated with early pregnancy particularly because of the conspicuous size of granulosa luteal cells. Since no embryonic sacs were found, it is then also not surprising that the endometrium possesses different histologic features from those whose comparable corpora lutea were associated with early pregnancy (Figures 11-13). Perhaps this climaxes endometrial development before regression of corpus luteum occurs.

One of these specimens from an October catch (no. 20, Table 6) had a fresh corpus luteum with fibrin-filled cavity and unusual endometrium. The stroma beneath the surface epithelium had the typical hyalinization of the post partum state, yet, early secretory endometrium was found in deeper layers (Figure 22). Moreover, hemosiderin pigment was found. It would appear that this was the first and infertile ovulation after a recently past pregnancy which is further supported by the

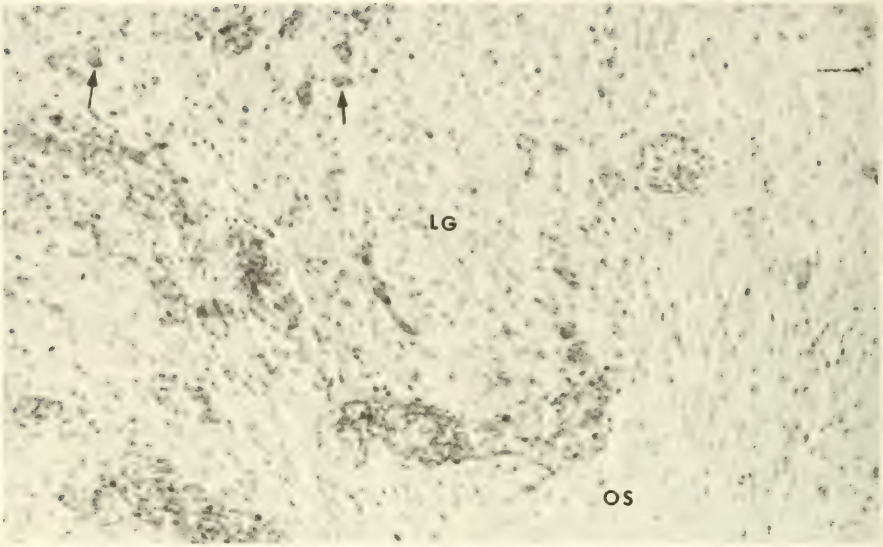


FIGURE 16.—Very fresh corpus luteum with focal hemorrhages (left), luteinized granulosa cells (LG) infiltrated by capillaries (arrows) sprouting from the ovarian stroma (OS) (no. 18, Table 7; hematoxylin and eosin × 400).

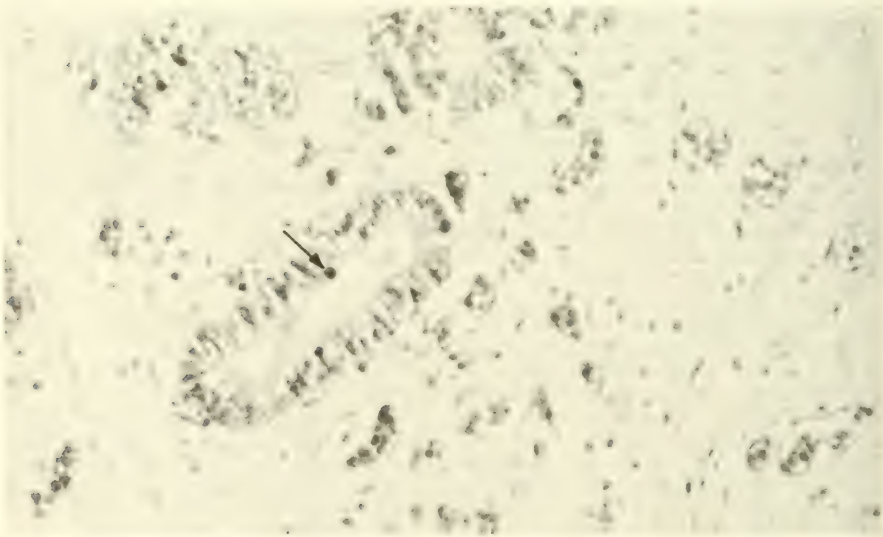


FIGURE 17.—Endometrium of specimen in Figure 16 with glandular mitosis at arrow. Note stromal edema (hematoxylin and eosin × 400).

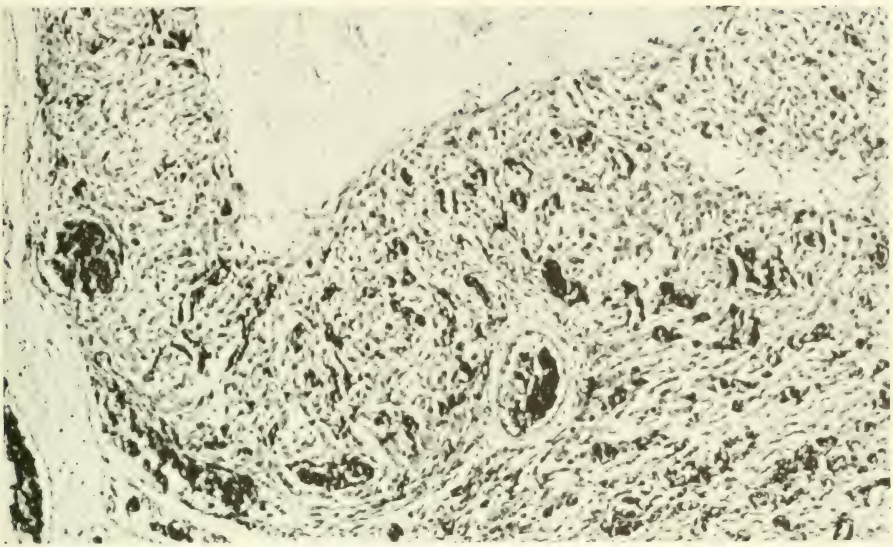


FIGURE 18.—Young corpus luteum in nonpregnant animal. Note central cavity (top) is filled with fibrin and granulosa layer is penetrated by capillaries (black). Size of granulosa lutein cells is much smaller than in Figure 11, an early pregnant specimen (no. 3, Table 7; hematoxylin and eosin × 100).

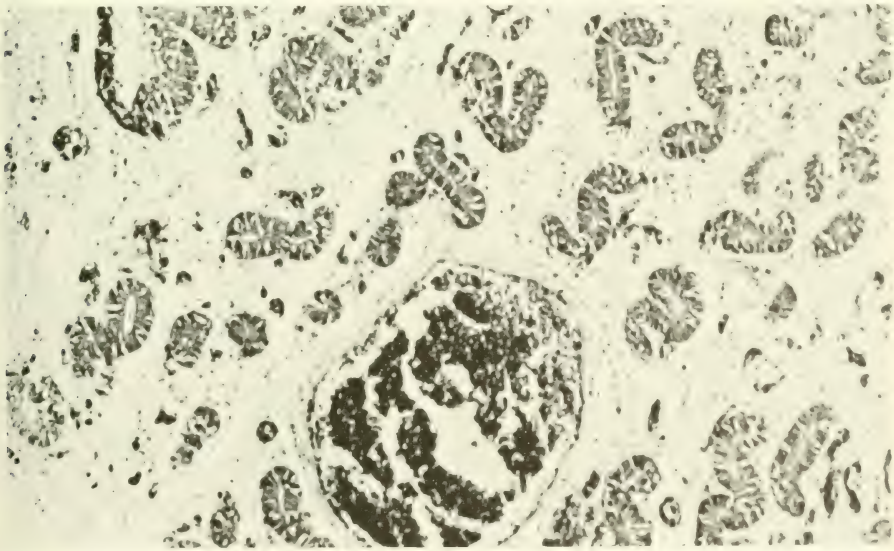


FIGURE 19.—Endometrium of same specimen as Figure 18 to show increased glandular coiling and earliest appearance of light cytoplasmic vacuoles in dark epithelial cells (hematoxylin and eosin × 100).

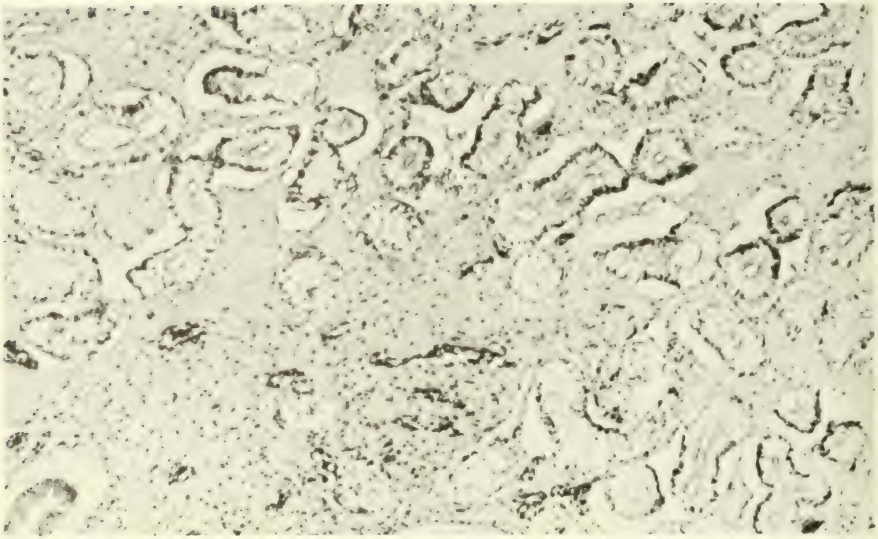


FIGURE 20.—Endometrium of nonpregnant *Stenella longirostris* with well-established corpus luteum, to show secretory vacuoles in endometrial glands as well as stromal edema (no. 10, Table 7; hematoxylin and eosin × 100).

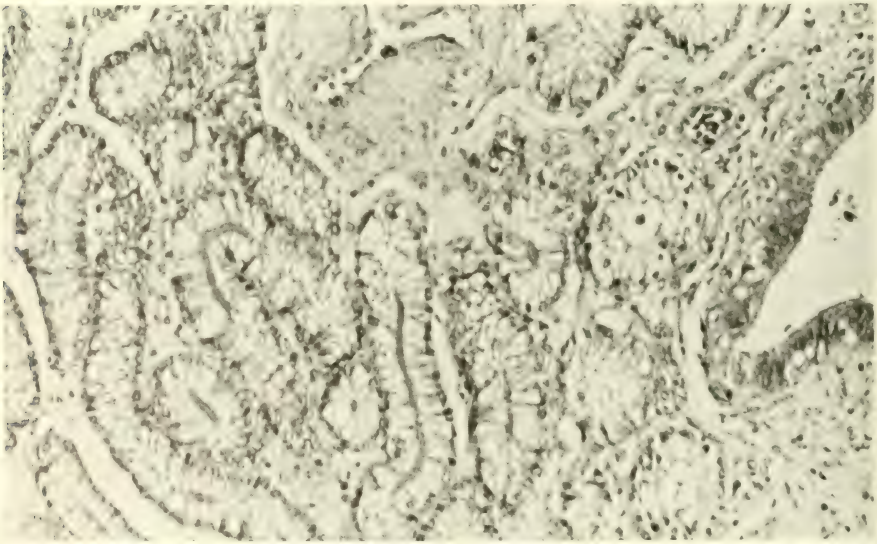


FIGURE 21.—Final stages of secretory change in endometrium of nonpregnant *Stenella longirostris* with advanced corpus luteum. Crowding of secretory glands occurs in stroma that has now lost its edema. No secretion in lumen. Endometrial cavity at right (no. 16, Table 7; hematoxylin and eosin × 100).

FIGURE 22.—Endometrium of presumably delivered *Stenella attenuata* whose ovary had a fresh corpus luteum. Endometrial cavity top left, hyalinized stroma (HyS) beneath surface epithelium and secretory glands (SG) beneath this layer (no. 20, Table 7; hematoxylin and eosin × 100).

marked discrepancy of the uterine horns (29 cm left; 18 cm right).

GROUP VIb.—These 15 animals (11 *S. longirostris*; 4 *S. attenuata*) were found to be nonpregnant but had well-established corpora lutea with completely organized cavities, the luteal cells appeared well supported (Table 8). Their lengths varied from 169 to 198 cm and uterine weights were between 110 and 580 g. One of these specimens had not been opened, was carefully dissected by us, and found to be nonpregnant. Again, most (12) were from February catches, many uteri had stretch marks from former pregnancy, and in two ovaries the corpus luteum was found on the right.

The secretory endometrium of almost all these

TABLE 8.—Group VIb: Experimental group with well-supported corpora lutea. Specimen no. 1-11 *Stenella longirostris*; no. 12-15 *S. attenuata*.

Specimen no.	Month and year of capture	Dolphin length (cm)	Uterus weight (g)	Left uterine horn				Right uterine horn			
				Length (cm)	Endometrial fold (mm)	Endometrial valley (mm)	Myometrium (mm)	Length (cm)	Endometrial fold (mm)	Endometrial valley (mm)	Myometrium (mm)
1	Feb. 1976	191	281	21	5.97	1.19	0.66	18	5.07	1.64	0.60
2	Feb. 1976	169	—	17	2.23	1.64	0.90	14	1.94	1.19	0.84
3	Feb. 1976	180	—	19	4.18	1.04	0.75	13	3.28	1.04	0.75
4	Feb. 1976	184	142	18	7.16	0.84	1.49	16	6.57	1.49	1.79
5	Feb. 1976	180	149	22	5.67	0.90	1.19	16	4.33	1.04	1.19
6	May 1976	178	268	24	4.48	1.04	1.94	19	2.84	0.75	1.34
7	Feb. 1976	180	194	20	3.58	1.34	1.34	16	3.73	1.94	0.90
8	Feb. 1976	178	227	21	4.18	0.75	1.19	13	3.28	1.19	1.04
9	Feb. 1976	181	148	16	3.58	1.19	1.34	11	3.28	1.19	1.19
10	Feb. 1976	170	117	18	4.48	1.04	1.04	15	3.88	1.04	1.49
11	Feb. 1976	181	166	21	1.79	0.90	1.19	12	2.99	1.04	1.04
			S. longirostris — Average	4.30	1.08	1.18			3.74	1.23	1.11
12	Feb. 1976	193	250	24	5.67	2.09	1.34	23	2.84	1.19	0.90
13	Feb. 1976	184	110	11	3.28	0.90	1.04	10	4.18	0.90	0.84
14	June 1977	185	240	22	2.39	1.19	1.79	17	1.79	0.60	1.88
15	Nov. 1975	198	580	37	5.67	1.49	2.09	21	6.87	1.49	2.39
			S. attenuata — Average	4.25	1.42	1.57			3.92	1.05	1.50

specimens showed great similarity with those shown in Figures 20 and 21. The amount of edema varied slightly and so did the glandular vacuolization. No secretion was found within the glands although frequently there was thick mucus covering the endometrial surface on gross examination. The luteal cells were supported, not degenerated but less plump than in early pregnancy. The only difference was the complete fibrosis of the central cavity, probably insufficient findings for a meaningful separation of some specimens from the previous group VIa. Of course, no capillary proliferation of the superficial endometrium, so typical of pregnancy was evident.

One specimen is probably misclassified (no. 15, Table 8). Not only is this the largest uterus (580 g) with pronounced stretch marks (Figure 23) but also it exhibits a differing histologic appearance of the endometrium (Figure 24). This shows acute endometritis in a mucosa which otherwise had all of the characteristics of pregnancy. The corpus luteum was well supported with large plump cells. In all likelihood this *S. attenuata* had very recently delivered. This is from a November catch and it is impossible to determine whether this represented a full-term pregnancy since Perrin et al. (1976) showed that calving does occur in this species in the winter, although less commonly. It may well be that this inflammatory exudate in the superficial endometrial regions represents the normal immediately post partum event. This would explain the persistence of an active corpus

FIGURE 23.—Uterus of recently delivered *Stenella attenuata*, no. 15, Table 8. Note stretch marks of left horn, congestion and disparate size of horns.

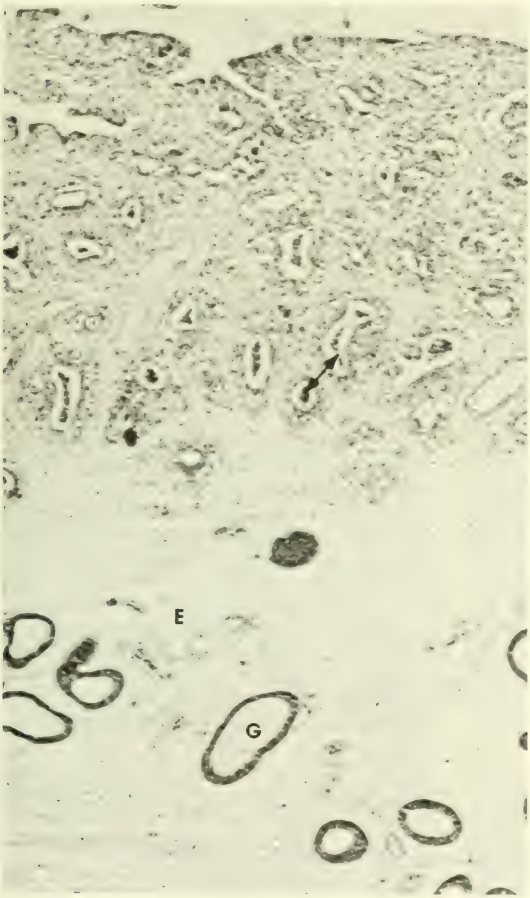


FIGURE 24.—Endometrium of uterus in Figure 23. The marked stromal edema (E) and distended glands (G) of basal endometrium are typical of late pregnancy. The superficial endometrium is infiltrated by polymorphonuclear leukocytes that exude into the glandular lumina (arrow). No surface stromal hyalinization has yet taken place. The former interdigitation of placental villi with surface endometrium can be imagined from the irregularities the surface presents (hematoxylin and eosin × 100).

luteum, presumably destined to involute shortly.

GROUP VIc.—This composes 15 animals (8 *S. longirostris*; 7 *S. attenuata*) measuring 162-193 cm whose features are listed in Table 9. These nonpregnant dolphins possessed histologically regressing corpora lutea. Eight animals in fact had corpora albicantia and were probably misclassified by the gross observations because the corpus luteum in each case was recently involuted, had still some vascularization and microscopic inflammation. Similarly, the endometria in these specimens usually had inflammation and hyalinization and were most likely recently delivered. This is further supported by the disparity in uterine horns. These animals were not listed as lactating either because this feature had been overlooked or perhaps the calves had died or were aborted. This material does not allow this differentiation.

Six of the remaining seven animals had corpora lutea with histologic signs of early degeneration. Two had late secretory endometrium and this would likely to have involuted upon further regression of the corpus luteum since pregnancy did not occur. Two animals had marked chronic en-

TABLE 9.—Group VIc: Experimental group with degenerating corpora lutea. Specimen no. 1-8 *Stenella longirostris*; no. 9-15 *S. attenuata*.

Specimen no.	Month and year of capture	Dolphin length (cm)	Uterus weight (g)	Left horn of uterus				Right horn of uterus			
				Length (cm)	Endometrial fold (mm)	Endometrial valley (mm)	Myometrium (mm)	Length (cm)	Endometrial fold (mm)	Endometrial valley (mm)	Myometrium (mm)
1	Sept. 1976	162	250	32	5.22	1.19	2.24	15	3.88	1.19	1.64
2	Feb. 1976	175	252	25	10.14	2.09	1.19	12	—	—	1.04
3	May 1976	183	273	25	4.93	1.04	1.19	15	3.88	1.19	1.04
4	Feb. 1976	179	—	23	4.78	0.90	1.19	14	4.48	1.94	1.34
5	Feb. 1976	185	—	21	2.09	0.90	0.90	16	1.19	1.04	0.75
6	Feb. 1976	186	—	22	2.24	0.75	0.90	16	1.04	0.45	0.90
7	Feb. 1976	186	291	25	5.37	1.19	1.34	14	3.58	0.90	1.04
8	Mar. 1976	189	197	17	5.37	1.19	1.64	13	3.28	1.04	1.04
				S. longirostris — Average	5.02	1.16	1.32		3.05	1.11	1.10
9	Aug. 1976	172	145	—	1.64	0.45	0.90	—	2.09	0.60	0.60
10	Feb. 1976	180	122	18	5.79	1.34	1.64	15	6.57	1.19	1.04
11	Feb. 1976	185	—	23	3.13	0.90	1.34	18	2.39	0.60	1.04
12	May 1976	191	205	18	4.18	0.75	1.79	18	2.39	0.60	1.79
13	June 1976	193	375	22	8.80	1.94	2.09	15	6.42	1.79	1.79
14	Aug. 1976	179	356	30	6.57	1.04	1.79	16	5.07	0.75	0.90
15	Apr. 1976	185	305	25	4.18	0.90	1.49	13	3.28	0.90	1.64
				S. attenuata — Average	4.90	1.05	1.60		4.03	0.92	1.26

dometritis. Two others had marked endometrial stromal edema in addition to having horns of different lengths. The possibility of abortion exists in these animals but this cannot be proven. Finally, one animal of this heterogeneous group (no. 12, Table 9) had equal uterine horns (18 cm) and possessed corpora albicantia in addition to a degenerating right-sided corpus luteum. The endometrium with hyalinization and capillary development suggested recent pregnancy but because of the size of the uterus (205 g) it appears likely that a recent right-sided pregnancy had ended in abortion.

DISCUSSION

Although conclusive proof is lacking, the results support the notion that dolphins may ovulate spontaneously, at least at times. Control material of different reproductive phases (96 specimens) of the two species of dolphin investigated, the eastern spinner dolphin, *S. longirostris*, and the spotted dolphin, *S. attenuata*, provided a life history of the macroscopic and microscopic events in the uteri and ovaries of these species for the first time. The principal findings were the following: In three immature animals neither corpora lutea nor corpora albicantia were present in the ovaries but Graafian follicles were forming. The endometrium had tubular glands. Six mature animals without corpus luteum all were found to have one or more corpus albicans, the horns were disparate in size, five had stretch marks as an excellent sign of former pregnancy, in most the inactive endometrium possessed inflammatory cells, hyalinization, had hemosiderin macrophages as indications of former pregnancy. Eleven of twelve early pregnant animals with embryonic sizes of 1-53 mm had the pregnancy in the left horn; one in the right on which side the corpus luteum was also located. The endometrium of the earliest pregnancy had characteristic changes that should allow pregnancy diagnosis even if the embryo is overlooked or lost. Six late pregnant specimens had their corpus luteum in the left ovary, typical epitheliochorial implantation and again characteristic endometrial histology. Eleven lactating females were studied, none of which had a corpus luteum, but all possessed at least one corpus albicans which was in various stages of degeneration. The endometrium showed typical regressive changes with hyalinization, chronic inflammation, and hemosiderin. These features will also allow categorization of uteri from females with unknown reproductive state in future studies. Of the 58 animals with macroscopically diagnosed corpora lutea and no detectable pregnancy, only 43 in fact had an active corpus luteum, the remaining 15 specimens had corpora albicantia in various stages of regression. Three corpora lutea were on the right, the remaining 40 were on the left, confirming the usual finding of Cetacea that the left side predominates in reproduction. When a correlation was sought between the development of the corpus luteum and endometrial changes a well-delineated cycle of proliferation and edema to secretory stages emerged. No changes indicative of early pregnancy were seen and three intact uteri contained no embryos. Thus, clearly, ovulation does occur without pregnancy ensuing. In three

specimens the findings are consistent with abortion, two had marked endometritis. These latter findings are summarized in Table 10.

TABLE 10.—Group VI: Summary of experimental, nonpregnant animals; 38 *Stenella longirostris*, 20 *S. attenuata*.

S. longirostris:		
19	(50%)	Fresh corpus luteum
11	(29%)	Well-established corpus luteum
8	(21%)	Degenerating corpus luteum—wrong gross diagnosis (2 endometritis; 2 unimplanted abortion?)
S. attenuata:		
9	(45%)	Fresh corpus luteum
3	(15%)	Well-established corpus luteum
1	(5%)	Misclassified, recently delivered
7	(35%)	Degenerating corpus luteum—wrong gross diagnosis (1 recent abortion?)

The findings of Perrin et al. (1976, 1977) indicate that over 90% of female genital tracts of *S. longirostris* and *S. attenuata* contain a corpus luteum because of their pregnancy. The possibility that abortions of implanted pregnancies occur frequently can be ruled out from the histologic appearance of the endometria in the majority of the specimens from the experimental group. Early embryonic death remains a possibility although no evidence can be adduced for this. The present study provides strong evidence that spontaneous ovulation may occur in these species, at least that the presence of a corpus luteum is not indicative of pregnancy. Moreover, recent and as yet unpublished results from our laboratory (J. Sawyer) have identified hormonally the occurrence of spontaneous ovulation in a *Delphinus delphis* female that was kept in isolation. Evidence for regression of corpora lutea in nonfertile cycles was also found in our experimental group. It is possible then that either ovulation is induced in a majority of cycles or that a majority of dolphins become pregnant when ovulating. In either case, it is not likely that a count of corpora albicantia in dolphin ovaries accurately reflects the number of past pregnancies. We were unable to differentiate with certainty between the histologic appearance of a corpus luteum of early pregnancy and one from nonpregnant animals and cannot accept the alleged feasibility of the diagnosis of pregnancy from the histology of only a corpus luteum. The endometrial histology is a better guide. Whereas accessory corpora lutea have been found in other odontocetes (Brodie 1972), no such structures were encountered in the genital tracts of these two *Stenella* species.

It would be useful to know from aquaria with accurate historical information and pathologic study at death whether older females that have been kept in isolation since youth possess corpora albicantia. Inasmuch as the question of artificial insemination of exhibited animals has been raised in the past (Hill and Gilmartin 1977) it can be concluded that it would appear feasible without the need of superovulation.

From a practical standpoint it is suggested that the following points be considered in future studies. First, it would have been helpful to have had a histologic sample of mammary gland and vagina in all specimens to enhance histologic correlations. Moreover, inasmuch as the hormonal cycle of *D. delphis* is now being defined by modern endocrine techniques undertaken by sequential sampling of captive specimens it may be useful for future studies to save, for endocrine analysis, an aliquot of frozen serum. Potentially, such a study would clarify the status of equivocal corpora lutea. At the same time storage of fetal serum would allow insight into the fetal endocrine behavior which is known to differ so markedly between species. Perhaps such comparative studies will ultimately give additional insight into the phylogenetic descendency of Cetacea.

This study extends the sparse literature that exists on the morphology of the female reproductive organs. In general, the endometrial cycle is similar to that illustrated schematically for several whales (Slijper 1966) and for *Globiocephala melaena* (Harrison 1949). In this latter species Harrison (1949) also described the small superficial anastomosing vessels beneath the uterine epithelium and, in three recently ovulated specimens, he was unable to identify products of conception. In a later contribution, Harrison et al. (1969) suggested that while ovulation in *Tursiops truncatus* appears to be of a reflex nature, that of *S. graffmani* and *Lagenorhynchus obliquidens* may be spontaneous as in *G. melaena*. Our own findings cited above suggest, however, that in *D. delphis* spontaneous ovulation occurs and one wonders whether this then may not be the rule in Cetacea. A resolution can come only from longitudinal endocrine studies of isolated females from different species. Finally, as was the case in most other studies of the morphology of Cetacean reproductive organs, we observed no significant pathologic features in these specimens other than the endometritis described and occasional parametrial parasitic granulomata.

ACKNOWLEDGMENTS

The encouragement and constructive criticism of W. F. Perrin is warmly acknowledged. The study was performed under contract NAS07-35234. The original slides, additional data, photographs, negatives, and an expanded manuscript are on file at the Southwest Fisheries Center, La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, Calif.

LITERATURE CITED

BRODIE, P. F.
1972. Significance of accessory corpora lutea in odontocetes with reference to *Delphinapterus leucas*. J. Mammal. 53:614-616.

ENGLAND, B. G., W. C. FOOTE, D. H. MATTHEWS, A. G. CARDOZO, AND S. RIERA.
1969. Ovulation and corpus luteum function in the llama (*Lama glama*). J. Endocrinol. 45:505-513.

HARRISON, R. J.
1949. Observations on the female reproductive organs of the ca'aing whale, *Globiocephala melaena* Traill. J. Anat. 83:238-253.
1977. Ovarian appearance and histology in *Tursiops truncatus*. *In* S. H. Ridgway and K. Benirschke (editors), Breeding dolphins, present status, suggestions for the future, p. 195-204. U.S. Mar. Mammal Comm. Rep. MMC 76-07; available U.S. Dep. Commer., Natl. Tech. Inf. Serv. as PB 273-73.

HARRISON, R. J., R. C. BOICE, AND R. L. BROWNELL.
1969. Reproduction in wild and captive dolphins. Nature (Lond.) 222:1143-1147.

HILL, H. G., AND W. G. GILMARTIN.
1977. Collection and storage of semen from dolphins. *In* S. H. Ridgway and K. Benirschke (editors), Breeding dolphins, present status, suggestions for the future, p. 205-210. U.S. Mar. Mammal Comm. Rep. MMC 76-07; available U.S. Dep. Commer., Natl. Tech. Inf. Serv. as PB 273-73.

JÖCHLE, W.
1973. Coitus-induced ovulation. Contraception 7:523-564.

PERRIN, W. F., J. M. COE, AND J. R. ZWEIFEL.
1976. Growth and reproduction of the spotted porpoise, *Stenella attenuata*, in the offshore eastern tropical Pacific. Fish. Bull., U.S. 74:229-269.

PERRIN, W. F., D. B. HOLTS, AND R. B. MILLER.
1977. Growth and reproduction of the eastern spinner dolphin, a geographical form of *Stenella longirostris* in the eastern tropical Pacific. Fish. Bull., U.S. 75:725-750.

SLIJPER, E. J.
1966. Functional morphology of the reproductive system in Cetacea. *In* K. S. Norris (editor), Whales, dolphins, and porpoises, p. 277-318. Univ. Calif. Press, Berkeley and Los Ang.

A LARGE, OPENING-CLOSING MIDWATER TRAWL FOR SAMPLING OCEANIC NEKTON, AND COMPARISON OF CATCHES WITH AN ISAACS-KIDD MIDWATER TRAWL

Avoidance of nets by agile micronekton and nekton is one of the major problems with small midwater trawls routinely used for oceanic sampling by oceanographers and marine biologists (e.g., Harrisson 1967; Pearcy 1975; Roper 1977). A major advantage of small trawls is that they can be equipped with opening-closing devices so that samples can be ascribed to discrete depths. This capability is especially important for sampling deep water where densities of animals are low. An opening-closing rectangular midwater trawl with a mouth area of about 25 m^2 is the largest opening-closing net described (Baker et al. 1973). Another important advantage of small nets is that they can be used from most oceanographic vessels.

Large, commercial-size midwater trawls used to sample oceanic micronekton (Berry and Perkins 1966; Harrisson 1967; Taylor 1968; Clarke 1973, 1974; Krefft 1974; Roper 1977) are usually not evaded as successfully by nektonic animals. Big nets which filter large volumes of water have the added advantage of catching enough animals to characterize species and size composition from sparsely populated waters. However, these large nets lack opening-closing capability, and most oceanographic research vessels are unable to handle large nets, otter doors, and bridles (Pearcy 1975).

This paper describes a 50 m^2 pelagic trawl especially designed for use with an opening-closing cod end, attempts to evaluate its performance, and compares its catches of mesopelagic fishes and cephalopods with those from a 5.4 m^2 Isaacs-Kidd midwater trawl.

Midwater Trawl Description and Operation

The midwater or pelagic trawl was designed by G. Loverich, Nor'Eastern Trawl Systems, Inc.,[1] Bainbridge Island, Wash., for sampling mesopelagic fishes and cephalopods in conjunction with a 1 m^2 five-net opening-closing device which is attached to the cod end of the trawl (Figure 1). The body of the trawl is lined throughout with 19 mm (¾ in) stretch mesh. The net is 42 m long and was constructed with a gradual taper from mouth to cod end in order to provide a large netting area for filtration in order to reduce the water velocity through the meshes, stagnation and hang-up of animals on the netting, and extrusion of animals through the netting. The wings of the trawl are made of large mesh (292 mm). It was assumed that micronekton (fishes, squids, and shrimps up to 200 mm in length) escape or pass through this large mesh rather than lead into the trawl body, giving an effective diameter of the net for micronekton equivalent to the small mesh body of the trawl. Unfortunately data do not exist to evaluate herding or leading of oceanic micronekton by the wings of trawls.

The trawl has six seams with four identical panels for the top and bottom (wing, body, and intermediate) two identical side (wing, body, and intermediate) panels, and four cod end panels (Figure 2). The meshes were hung at 29.3% in both directions to allow formation of square openings and laced to make six seamlines. Two riblines are located along the middle of the side panels and extend to the opening-closing device.

A 1 m^2 Multiple Plankton Sampler (MPS) with five separate nets, each 4.6 m long (see Pearcy et al. 1977 for details), was used as an opening-closing cod end device on the trawl. The levers for release of the five nets of the sampler are actuated by a modular timer which employed a crystal oscillator and a binary series of counters for selection of release times (Evans 1975). The timer is mounted on the MPS, started as the trawl is launched, and is set to give the trawl time to stabilize at a selected towing depth before net 1 is released (usually 30-60 min). Thus the first net fishes obliquely from the surface to the fishing depth of net 2. The four remaining nets (nets 2-5) all fish the same amount of time on a given tow (usually 40 min), either at the same depth (horizontal series) or at different depths (vertically stratified series).

The footrope and headrope are each 28.6 m of 16

[1]Reference to trade names or commercial firms does not imply endorsement by the National Marine Fisheries Service, NOAA.

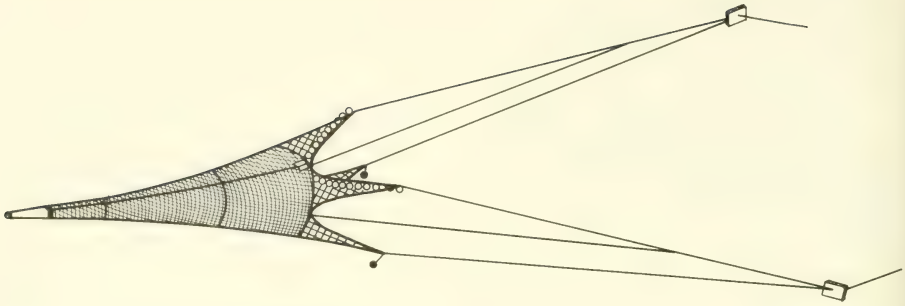


FIGURE 1.—Sketch of the pelagic trawl in operation.

mm poly-Dacron rope. The wings are of #60 thread, the body of #3 thread, the intermediate of #4 thread, and the cod end of #6 thread. Nineteen 25.4 cm (diameter) aluminum floats (good to 1,000 m) are attached to the headrope. Galvanized chain is attached to the footrope and one 23 kg lead ball is attached to the tip of each of the bottom wings. The bridles to the bottom wings are 55 m long; bridles to the upper wing are 36 m long, and the middle bridle is 47 m long (Figure 1).

The trawl was designed to be towed with 1.5-1.8 × 2.4-2.7 m (5 × 8 ft or 6 × 9 ft) otter doors. A scale model of the trawl was first constructed and tested in a tank to test its design and performance.

Observations were made on the trawl by divers during trials in Puget Sound using 1.8 × 2.7 m doors and towing speeds of 1.0 to 1.6 m/s at depths of about 12 m. The towing characteristics of the net were observed and the number of floats needed to provide neutral buoyancy to the cod end opening-closing device was determined by trial. At a towing speed of 1.6 m/s the vertical opening of the mouth was measured to be about 8 m and the body of the trawl was observed to be nearly circular and about 8 m in diameter, providing an estimate of about 50 m^2 for the cross-sectional area of the fine mesh netting of the trawl body.

The depth that each net fished was determined from the depth-modulated signal from an acoustical pinger mounted on the headrope of the trawl, a hydrophone towed from the vessel, and a graphic recorder. An EG&G pinger was used initially but was replaced with an Institute of Oceanographic Sciences (IOS) 0-683 m (0-100 atmospheres pressure) acoustical net monitoring system (Baker et al. 1973) with an overall accuracy of 0.1% of the full depth range.

Methods

A timer-actuated ejection device was used as a method to provide some information on the flushing rate through the body of the trawl. This device, similar to the one described by Pearcy et al. (1977), has a modular timer (Evans 1975) to release the contents of two 1.3 l chambers. It was hung from the headrope inside the trawl mouth and its contents were ejected against the 19 mm mesh. Preserved juvenile salmon (10-20 cm total length) were released into the net at intervals of 5, 10, 15, or 25 min before closure of net 1 and opening of net 2.

The pelagic trawl-MPS combination was used on three chartered trawlers off Oregon. All vessels had net reels and used double-warp towing. A boom was used to launch and recover the MPS during 1975 and 1976 cruises. The vessel chartered in 1977 had a stern ramp, which greatly facilitated use of the pelagic trawl. Twelve tows were made in 1975 to test the monitoring equipment and to evaluate flushing of the net. Eight tows were made in 1976 and 10 in 1977. All tows were 110-130 km off the central Oregon coast; 18 of these tows provided the data for comparison of pelagic trawls and Isaacs-Kidd midwater trawls (IKMT's) (Table 1).

Tows were also made with a 5.4 m^2 IKMT with 10 mm stretch mesh and a 1 m^2 MPS opening-closing device (Pearcy et al. 1977) at 1.5-2.0 m/s at a similar location and within 10 days after each of three cruises that used the pelagic trawl (Table 1). Volume of water entering the IKMT was monitored with a modified TSK flowmeter on all tows. One of the purposes of these IKMT tows was to enable comparisons of the catches by the two different types of nets.

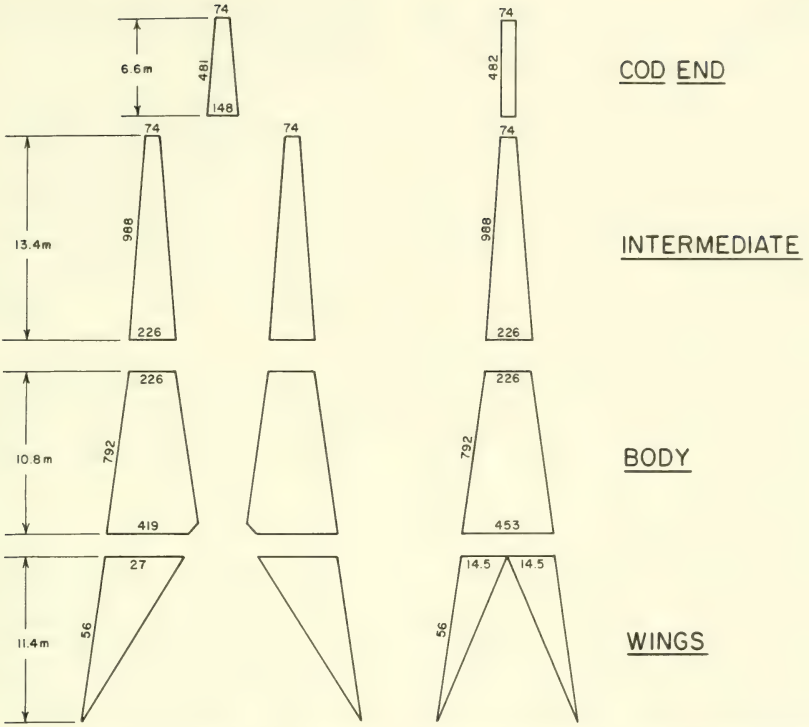


FIGURE 2.—Net plans for the pelagic trawl. Numbers on the net panels indicate number of meshes along the margins.

Collections were preserved in 10% Formalin at sea. In several instances large catches (>35 l) of the pelagic trawl were subsampled, but at least 14 l of the catch of each of the nets for discrete depths were preserved. Fishes and cephalopods were identified and measured [standard length (SL) of fishes and dorsal mantle length (DML) of squids].

TABLE 1.—Summary of pelagic trawl (PT) and Isaacs-Kidd midwater trawl (IKMT) tows made on the three "paired" cruises off Oregon.

Net	Dates	Vessel	No. Tows	Depth (m)	Time
	1975:				
PT	23 Sept.	*Betty-A*	1	340-360	Day
IKMT	12-16 Sept.	*Yaquina*	5	334-362	Day
	1976:				
PT	19-22 July	*Pacific Raider*	8	0-500	Day-night
IKMT	8-13 July	*Wecoma*	11	0-465	Day-night
	1977:				
PT	30 July-2 Aug.	*Excalibur*	9	185-365	Day-night
IKMT	8-10 Aug.	*Wecoma*	5	187-350	Day-night

Results

Flushing of the Pelagic Trawl

In Puget Sound, divers observed that dead salmon smolts released in the mouth of the trawl were never stuck against the netting in the forward part of the trawl where the meshes were taut from water pressure. Occasionally fish stalled against the mesh in the aft section of net where netting was less rigid, but these fish were easily dislodged and tumbled toward the cod end. Because live fishes usually swim away from the netting when inside a trawl, it seems unlikely that live, active fish would be pinned against the netting (G. Loverich[2]). Obviously, dead, preserved fish do not

[2]G. Loverich, Nor'Eastern Trawl Systems, Inc., Bainbridge Island, WA 98110, pers. commun. January 1979.

behave like live ones, but they do provide some information on flow characteristics through the net and how easily objects are pinned against the mesh.

The results of the release of preserved salmon smolts into the mouth of the pelagic trawl on two cruises in the open ocean are shown in Table 2. Ninety-seven percent of the fish released in the mouth were recovered in cod end nets 1 and 2 within 5-25 min after release: 82% were recovered in net 1. These data indicate an average residence time of preserved fish of <10 min in the body of the trawl.

If live animals were delayed by 10-120 min in passing through the net into the cod end, then the number of animals found in different cod end nets may vary, with largest numbers in latter nets and fewest in the first or second net as found by Foxton (1970) and Donaldson (1975) in other cod end opening-closing devices. Coefficients of concordance, W, (Tate and Clelland 1957) were not significant ($P>0.2$) for rank order of abundance of fishes (12 tows), squids (10 tows), and *Stenobrachius leucopsarus*, the most common fish (10 tows) for nets 2-5 that sampled equal time intervals and also caught at least 10 of each of these three types of animals. Similar nonparametric tests of the rank order of abundance of 15 common species were not significant for nets 2-5 of nine tows with same net, where each net fished 2 h (Willis 1979). This lack of correlation of catch with net number provides no evidence for delay or stagnation of animals in the net over time periods of 10 min to 6 h. Characteristic species compositions or size-frequency distributions from specific depths (Willis and Pearcy[3]) also indicate that cod end catches are predominantly from the depths fished.

Entanglement or hang-up of fishes and cephalopods in the meshes of the trawl appeared to be restricted to a few types. Fishes such as the stomiatoid, *Tactostoma macropus*, were occasionally found hanging on the meshes of the trawl body by their teeth. Soft-bodied cephalopods, such as *Chiroteuthis calyx* and *Vampyroteuthis infernalis*, were sometimes entangled in the mesh. The number of animals hung on the net after a tow was always a small fraction of those in the cod ends. These entangled animals that are retained in the net from one tow are probably washed-down into the first net of the next trawl. Since this first net is the one that fishes obliquely from the surface to the selected depth of sampling, it is not usually used in studying vertical distribution of animals.

TABLE 2.—Results of release of preserved salmon from the ejection device in front of the pelagic trawl. All tows were horizontal at 2.5-3.0 kn. ND means no data.

Vessel	Minutes that ejection device was set to go off before closure of net 1	Interval between closure of nets 2-5 (min)	No. of fish in net: 1	2	3	4	5	No. recovered/no. used
Betty-A	10	15	35	0	0	(1)	(1)	ND
	10	15	35	0	0	0	(1)	ND
	10	15	30	3	0	0	0	ND
	25	20	36	0	0	0	0	ND
Pacific Raider	5	40	30	24	1	4	2	61/65
	10	40	[2]0	[2]34	[2]2	[2]0	[2]7	43/60
	10	40	33	25	0	0	0	58/60
	15	40	49	1	0	0	2	52/59
Percent recovered in each net			82	15	1	1	1	

[1]Net failed to close
[2]Cod end of trawl was twisted. This trawl was excluded from percentage calculations.

Pelagic Trawl-IKMT Comparisons

The 17 pelagic trawls caught almost twice as many species of fishes, and about the same number of cephalopod species as the 16 IKMT's during the two major cruises in 1976 and 1977. These differences are mainly due to the large volumes of water filtered by the pelagic trawl and consequently the large number of individuals captured.

One of the most significant differences between the catches was the presence of some fish species in the pelagic trawl and their complete absence in the IKMT catches (number caught-vessel, where PR = *Pacific Raider* and EX = *Excalibur*): *Aphanophus carbo* (3-PR), *Merluccius productus* (3-PR), *Idiacanthus antrostomus* (23-PR), *Aristostomias scintillans* (24-PR, 6-EX), Macrouridae (5-PR), *Lestidium ringens* (37-EX), *Nansenia candida* (22-EX), *Symbolophorus californiensis* (5-EX). In over 2,000 (2, 2.5, and 3 m mouth opening) IKMT tows made off Oregon since 1961, we have never before captured *Aphanophus carbo* or *M. productus* in oceanic waters. These fishes were large (436-570 mm) and presumably always avoid IKMT's.

Length-Frequency Comparisons

Significant differences [$P<0.5$, Kolmogorov-Smirov (K-S) two sample comparisons (Tate and Clelland 1957)] were found in the size-frequency

[3]Willis, J. M., and W. G. Pearcy. Spatial and temporal variation in the population size structure of three lanternfishes (Myctophidae) off Oregon. Unpubl. manuscr.

distributions of four common species (where $n>50$ for fishes for each of the two nets, and $n>20$ for squid) for: *Stenobranchius leucopsarus* in two of the three comparisons, *Diaphus theta* in one of two comparisons, and *Tarletonbeania crenularis* in two of two comparisons. In all instances where length distributions differed, the pelagic trawl caught an appreciably higher percentage of large animals. Even though the one K-S test for the squid *Gonatus pyros* was not significant (because of small numbers caught in the IKMT), 15% of numbers of this squid from the pelagic trawl were >35 mm DML and no animals >35 mm were caught in the IKMT.

Length-frequency distributions for *S. leucopsarus* and *T. crenularis* from both trawls (Figure 3) show that large lanternfishes are clearly undersampled by the IKMT. The modes composed of fishes >45 mm, which are prominent in pelagic trawl catches, are absent in IKMT catches.

Another notable example of differences between catches of large fish in these collections were captures of *Tactostoma macropus*. Few large individuals (>250 mm) have been collected in IKMT tows off Oregon. Three tows with the pelagic trawl at depths of 470-1,070 m in 1978, however, captured many large fish. Twenty-nine percent of the *T. macropus* caught in these pelagic trawl collections were >250 mm, compared with only 8.2% in 252 IKMT tows to 500 m depth or deeper during previous years.

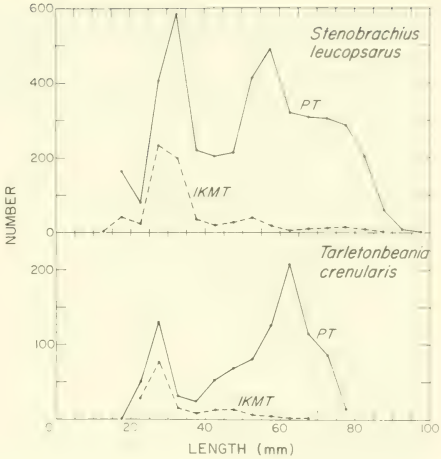


FIGURE 3.—Length-frequency distribution for *Stenobrachius leucopsarus* and *Tarletonbeania crenularis* in pelagic trawl and IKMT collections, July 1976, 0-500 m.

Effective Cross-Sectional Area of the Pelagic Trawl

The cross-sectional area of the pelagic trawl was indirectly estimated from the catches of four species of lanternfishes caught in both the pelagic trawl and IKMT on the three "paired" cruises (Table 1) to see how it compared with the divers' estimates of 50 m². The following equation was used:

$$A = \frac{C_1 V}{C_2 D}$$

where A = area in square meters,
C_1 = number of fish caught by pelagic trawl,
V = volume filtered by the IKMT, in cubic meters,
C_2 = number of fish caught by the IKMT,
D = distance trawled by the pelagic trawl in meters.

The volume of water filtered by the IKMT was calculated from a flowmeter mounted in the MPS and monitored aboard ship via electrical cable (see Pearcy et al. 1977). Distances trawled by the pelagic trawl were calculated from ship speed (based on Loran readings) and the duration of the tow. In each comparison, tows and nets selected fished similar depths at the same time of day. The mouth area estimated in this way varied from 19 to 3,161 m² with a median value between 48 and 62 m² (Table 3). The smallest area (19 m²), for *D. theta*, can be largely explained by the retention of small fish (10-15 mm) in the IKMT but not by the slightly larger mesh of the pelagic trawl. This is the only obvious example of differences in size-frequency distributions that can be explained by escapement of small fish. The large values of mouth area may result from different population densities of two species at the times of sampling during the 1977 cruises.

The present study indicates that large nets usually catch more individuals, and usually, but not always, more species and larger animals than small IKMT-type nets. Detailed quantitative comparisons are needed with nets of known cross-sectional areas, with similar mesh size, at the same depths and locations (Roper 1977). Large nets will never replace the smaller IKMT's and rectangular midwater trawls because of the specialized equipment needed to launch and re-

TABLE 3.—Estimates of the effective mouth size of the pelagic trawl (PT) based on estimated distance trawled (speed × time), the catches of four lanternfishes, and the catches of four lanternfishes and volumes for IKMT's on "paired" cruises.

Item	*Stenobrachius leucopsarus*	*Diaphus theta*	*Tarletonbeania crenularis*	*Protomyctophum thompsoni*
1975—1 PT, 5 IKMT, 340-350 m, day:				
Distance trawled by PT = 23,718 m				
Vol. filtered by IKMT = 435,210 m^3				
No. caught in PT	2,121	216	146	218
No. caught in IKMT	816	212	61	123
Effective mouth area, m^2	48	19	44	32
1976—8 PT, 11 IKMT, 0-350 m, day/night:				
Distance trawled by PT = 148,425 m				
Vol. filtered by IKMT = 1,525,860 m^3				
No. caught in PT	4,306	1,663	1,007	183
No. caught in IKMT	718	644	167	60
Effective mouth area, m^2	62	27	62	31
1977—2 PT, 3 IKMT, 290-325 m, day/night:				
Distance trawled by PT = 18,931 m				
Vol. filtered by IKMT = 630,385 m^3				
No. caught in PT	2,658	149	388	192
No. caught in IKMT	28	4	2	100
Effective mouth area, m^2	3,161	1,240	646	64

cover large nets from oceanographic vessels. We need to compare catches of different-sized trawls, however, in order to evaluate biases and to learn what portions of the plankton-micronekton-nekton spectrum are effectively sampled by different nets.

Acknowledgments

This research was supported by the Office of Naval Research through Contract N00017-76-C-0067 under Project NR083-102. I am grateful to M. Willis, D. Stein, and R. Mesecar for comments on the manuscript, to J. Fisher, F. Evans, and D. Stein for invaluable help at sea, and to G. Loverich for design and evaluation of the pelagic trawl.

References

BAKER, A. DE C., M. R. CLARKE, AND M. J. HARRIS.
1973. The N.I.O. combination net (RMT 1 + 8) and further developments of rectangular midwater trawls. J. Mar. Biol. Assoc. U.K. 53:167-184.

BERRY, F. H., AND H. C. PERKINS.
1966. Survey of pelagic fishes of the California Current area. U.S. Fish Wildl. Serv., Fish. Bull. 65:625-682.

CLARKE, T. A.
1973. Some aspects of the ecology of lanternfishes (Myctophidae) in the Pacific Ocean near Hawaii. Fish. Bull., U.S. 71:401-434.
1974. Some aspects of the ecology of stomiatoid fishes in the Pacific Ocean near Hawaii. Fish. Bull., U.S. 72:337-351.

DONALDSON, H. A.
1975. Vertical distribution and feeding of sergestid shrimps (Decapoda: Natantia) collected near Bermuda. Mar. Biol. (Berl.) 31:37-50.

EVANS, F.
1975. Universal modular timer. Exposure 3:8-11.

FOXTON, P.
1970. The vertical distribution of pelagic decapods (Crustacea: Natantia) collected on the SOND cruise 1965. J. Mar. Biol. Assoc. U.K. 50:939-960.

HARRISSON, C. M. H.
1967. On methods for sampling mesopelagic fishes. Symp. Zool. Soc. Lond. 19:71-126.

KREFFT, G.
1974. Investigations on midwater fish in the Atlantic Ocean. Ber. dtsch. wiss. Komm. Meeresforsch., Neue Folge, 23:226-254.

PEARCY, W. G. (editor).
1975. Workshop on problems of assessing populations of nekton. Off. Nav. Res. Rep. ACR 211, 30 p.

PEARCY, W. G., E. E. KRYGIER, R. MESECAR, AND F. RAMSEY.
1977. Vertical distribution and migration of oceanic micronekton off Oregon. Deep-Sea Res. 24:223-245.

PEARCY, W. G., AND R. M. LAURS.
1966. Vertical migration and distribution of mesopelagic fishes off Oregon. Deep-Sea Res. 13:153-165.

ROPER, C. F. E.
1977. Comparative captures of pelagic cephalopods by midwater trawls. Symp. Zool. Soc. Lond. 38:61-87.

TATE, M. W., AND R. C. CLELLAND.
1957. Nonparametic and shortcut statistics in the social, biological, and medical sciences. Interstate Printers and Publishers, Inc., Danville, Ill., 171 p.

TAYLOR, F. H. C.
1968. The relationship of midwater trawl catches to sound scattering layers off the coast of northern British Columbia. J. Fish. Res. Board Can. 25:457-472.

WILLIS, J. M.
1979. Vertical distribution and migration of fishes from the lower mesopelagic zone off Oregon. M.S. Thesis, Oregon State Univ., Corvallis, 52 p.

WILLIAM G. PEARCY

School of Oceanography
Oregon State University
Corvallis, OR 97331

PASSIVE BEHAVIOR BY THE SPOTTED DOLPHIN, *STENELLA ATTENUATA*, IN TUNA PURSE SEINE NETS

The purse seining method of catching yellowfin tuna, *Thunnus albacares*, in association with schools of dolphins in the eastern tropical Pacific has been described by Perrin (1969). The primary target species, in order of importance, are the spotted dolphin, *Stenella attenuata*, and the spinner dolphin, *S. longirostris*, with occasional net sets made on schools of the common dolphin, *Delphinus delphis*. Schools of these dolphins ranging in size from 50 to several thousand are herded with speedboats and encircled with a purse seine net that is from 900 to 1,400 m long and as much as 130 m deep. After the dolphins are encircled, the bottom of the net is pursed, entrapping the mammals and any tuna that are associated with the school. Presently, neither the mechanisms nor the function of the close association of the yellowfin tuna with these schools of dolphins in the eastern tropical Pacific are clearly understood.

Studies of the behavior of dolphins while captive in a purse seine net were pursued during the chartered cruise of the commercial seiner MV *Elizabeth C. J.*, in October 1976 (Norris et al.[1]). Prior to this cruise, however, beginning in 1973, an intensive effort was made to develop net modifications and fishing techniques that would decrease the incidental killing of the mammals. Much of this effort was based upon general, to date unpublished, observations of captured dolphins and tuna made by National Marine Fisheries Service (NMFS) observers and technologists. One of the behavioral patterns of the spotted dolphin first noted by NMFS divers in 1973 and then recognized for its contribution to incidental mortality in 1975 is termed here "passive" behavior.

In the fall of 1975, NMFS chartered the purse seiner MV *Bold Contender* to carry on fishing gear dynamics research aimed at reducing incidental dolphin mortality. Part of this research included the evaluation of the use of a two-man inflatable raft as a dolphin rescue platform during and after the release procedure known as the "backdown" (Perrin 1969; Coe and Sousa 1972). A face mask and snorkel were worn by the person in the rescue raft to enable him to: 1) signal when tuna were approaching the release area during backdown, 2) keep track of sharks, particularly the oceanic whitetip shark, *Carcharinus longimanus*, both inside and outside of the net, 3) locate and release any stray dolphins and, 4) observe the dynamics of the net modification being tested during the cruise. Notes on the behavior of the captured dolphins during backdown were recorded after each of the 25 net sets in which the rescue raft was used. The underwater passive behavior of spotted dolphins was first noted in the eighth net set of the cruise and in 14 subsequent sets.

The passive behavior manifests itself in possibly two forms during the backdown release procedure. The first, which has been described as "rafting" by Norris et al. (see footnote 1), consists of groups of 5-50 or more spotted dolphins hanging tail-down at or near the surface and showing no overt reactions to their surroundings. This type of passive behavior can be seen from the deck of the seiner and is generally displayed from the time the net is pursed through the backdown (about ½ h). There is a steady increase in the number of rafting animals until backdown begins and then an apparent sharp decrease as backdown proceeds. The decrease in rafting may be due to the crowding and confusion during that period. Rafting behavior simplifies the effective release of these animals by backdown, because the net is actually pulled out from under the "raft" of dolphins as it remains relatively stationary in the water. Observations during the *Elizabeth C. J.* cruise showed that in every school of captured spotted dolphins some portion exhibited this behavior.

Dolphins in the captured school that are not in rafts during backdown are either actively swimming, usually in the horizontal plane directly away from the advancing wall of the net, or display the second manifestation of passive behavior. Prior to backdown, rafting dolphins are occasionally observed to sink tail first to depths up to 5 m before they swim awkwardly back to the surface, breathe, and sink again. During backdown, however, there are occasionally relatively large numbers of animals that sink to lie on the webbing (Figure 1) and many more that show signs of the sinking behavior and drop out of the rafts.

During backdowns on the *Elizabeth C. J.* cruise, from 3 to an estimated 75 spotted dolphins and, in one set, 2 bottlenose dolphins, *Tursiops truncatus*, were observed lying on the webbing in the bottom of the backdown channel. These animals, which

[1]Norris, K. S., W. E. Stuntz, and W. Rogers. 1978. The behavior of porpoises and tuna in the eastern tropical Pacific yellowfin tuna fishery - preliminary studies. Available U.S. Dep. Commer., Natl. Tech. Inf. Serv., Springfield, Va., as PB-283970, 86 p.

FIGURE 1.—Photograph taken during backdown of a tuna purse seiner showing three passive dolphins in the foreground. Note that the middle animal is resting on its dorsal fin. The four animals that are hanging flukes downward in the water are displaying the sinking behavior associated with rafting. (Photo courtesy of the Cooperative Dedicated Vessel Research Program, 1978.)

were making no apparent attempt to surface, were at depths that varied from 2 or 3 m to as much as 12 to 15 m. At first glance, the animals appeared to be struggling feebly, perhaps against the current being produced as the seine was pulled through the water during backdown. Their movements were weak and lacked the grace that long observation leads one to expect in dolphins. The majority of animals lying on the net in this manner were oriented with their heads toward the release area of the net (i.e., in the direction of the current), whereas the rafting and active animals were normally oriented away from the release area (i.e., heading into the current). After about 3-5 min, the passive dolphins began to rise singly or in two's and three's to breathe and were either backed out of the net or hand-released if the backdown procedure had already been terminated. No animals were seen returning to rest on the bottom of the net after surfacing.

Prior to promulgation and adoption of a federal regulation requiring use of a rescuer in a raft using a mask and snorkel, which resulted from the chartered cruise of the *Bold Contender*, this passive behavior probably was an important contributor to dolphin mortality in purse seines. When viewed from the deck of a speedboat tending the corkline in the dolphin-release area during backdown, these animals appeared to be dead if they were noticed at all, and as a result the release efforts were often prematurely terminated. Dolphins not released during the backdown have a high probability of being killed (Coe and DeBeer[2]).

The reasons for passive behavior in purse seine-caught spotted dolphins are not understood. The behavior has only rarely been observed in spinner dolphins in the tuna fishery. A similar behavior pattern has been described for two newly captured Hawaiian spinner dolphins during escape behavior experiments designed to delineate the dimensions of a dolphin release gate for possible use in purse seine nets (Perrin and Hunter 1972).

Animal trainers and biologists have noted what appears as similar behavior in individual captive dolphins of several species. Caldwell et al. (1966) reported prolonged inverted "resting or sleeping

[2]Coe, J. M., and J. DeBeer. 1977. Results of the 1976 twenty vessel test of two fine mesh systems to reduce incidental porpoise mortality in tuna purse seining. Unpubl. manuscr., 75 p. Southwest Fisheries Center, P.O. Box 271, La Jolla, CA 92038.

on the bottom of the tank" by a juvenile male Boutu, *Inia geoffrensis*. The occurrence of this behavior in *I. geoffrensis* and that observed in a juvenile male Atlantic bottlenose dolphin was frequent and apparently spontaneous (Caldwell[3]). Pryor[4] and Norris et al. (footnote 1) have noted instances where the passive-type behavior was presumably induced in training situations where *Tursiops* spp. were being "worked hard." These animals would go to the bottom of the tank, emit a quantity of air and might remain at the bottom for several minutes. Norris et al. hypothesized that this behavior may be similar to the "dearoused state" described by Delius (1970) for terrestrial animals, the most widely known example of which is the feigning of death by the Virginia opposum, *Didelphis marsupialis*. The major criticism (Norris et al.) of the dearousal hypothesis in the present situation would seem to concern the evolutionary value of such a response to a pelagic air breathing animal that would tend to sink toward the bottom in very deep water. One argument (Norris et al.) is that the situation which elicits dearousal (purse seining) has been a factor for only about 15-20 yr, and it is therefore not necessary to hypothesize an adaptive value for the behavior. To accept this hypothesis it would have to be assumed that the capability for dearousal has evolved in response to other circumstances.

A second hypothesis to explain this behavior relates to the effects of chase and capture on the physiology of the dolphins. Possibly indicative is the awkwardness of the swimming movements displayed by the animals while "passive." Harthoorn (1973) described the effects of chase and capture on large African mammals. Long chases using motor-driven vehicles result in a typical condition termed "capture myopathy." Capture myopathy is very common in the animals captured for zoos and often causes a delayed mortality. Symptoms include stiffness and awkward movements. The method of capturing dolphin schools involves a chase by speedboats that lasts up to 1.5 h and averages between 20 and 30 min. A chase of that duration is capable of causing myopathies in large terrestrial mammals which can be detected by measuring changes in blood serum enzyme levels (Harthoorn). A recent paper by Colgrove (1978) documents a suspected case of myopathy in a dolphin, *Tursiops gilli* = *T. truncatus*. This case of myopathy appears to have been induced by the stress of transporting the animal. Investigation of blood chemistry of passive dolphins may allow determination of whether capture myopathy does occur as a result of chase and capture during the tuna seining operation.

[3]David K. Caldwell, Director, Biocommunication and Marine Mammal Research Facility, University of Florida, Route 1, Box 121, St. Augustine, FL 32084, pers. commun. October 1979.

[4]Karen Pryor, former head animal trainer, Sea Life Park, Hawaii; present address: 28 East 10th Street, New York, NY 10003, pers. commun. November 1976.

Acknowledgments

We thank Jack Hailman, Kenneth Norris, and William Rogers for reviewing versions of this manuscript. The photograph was taken by Thomas Shay of the National Marine Fisheries Service during the Cooperative Dedicated Vessel Research Program cosponsored by the United States Tuna Foundation, the National Marine Fisheries Service, and the Marine Mammal Commission.

Literature Cited

CALDWELL, M. C., D. K. CALDWELL, AND W. E. EVANS.
1966. Sounds and behavior of captive Amazon freshwater dolphins, *Inia geoffrensis*. Los. Ang. Cty. Mus., Contrib. Sci. 108, 24 p.

COE, J., AND G. SOUSA.
1972. Removing porpoise from a tuna purse seine. Mar. Fish. Rev. 34(11-12):15-19.

COLGROVE, G. S.
1978. Suspected transportation-associated myopathy in a dolphin. J. Am. Vet. Med. Assoc. 173:1121-1123.

DELIUS, J. D.
1970. Irrelevant behavior, information processing and arousal homeostasis. Psychol. Forsch. 33:165-188.

HARTHOORN, A. M.
1973. Physiology and therapy of capture myopathy. 2d Annu. Rep. Transvaal Nat. Conserv. Div., Pretoria, Afr., p. 1-191.

PERRIN, W. F.
1969. Using porpoise to catch tuna. World Fishing 18(6):42-45.

PERRIN, W. F., AND J. R. HUNTER.
1972. Escape behavior of the Hawaiian spinner porpoise (*Stenella* cf. *S. longirostris*). Fish. Bull., U.S. 70:49-60.

JAMES M. COE
WARREN E. STUNTZ

Southwest Fisheries Center La Jolla Laboratory
National Marine Fisheries Service, NOAA
P.O. Box 271
La Jolla, CA 92038

EFFECTS OF LARGE PREDATORS ON THE FIELD CULTURE OF THE HARD CLAM, *MERCENARIA MERCENARIA*[1]

Individuals in the clam industry have used fences to keep the cownose ray, *Rhinoptera bonasus*, out of planted areas (Lewis[2]; Burton[3]). Tiller et al. (1952) indicated losses due to skates in planted holding areas and stated that "One man reported the loss of 600 bushels of small clams in two nights during 1948...." Merriner and Smith[4] stated that cownose ray predation is a serious problem on oyster and clam grounds in Chesapeake Bay. From these observations it is clear that such large predators could be a significant deterrent to the culture of clams from Delaware Bay southward along the Atlantic coast.

The present study continues a program designed to evaluate methods of protecting areas seeded with young *Mercenaria mercenaria*. The initial portion of the study outlined the interactive effects of pens, gravel, current baffles and crab traps on the first year's growth and survival (Kraeuter and Castagna 1977). The results of the second year study on the interactive effects of these manipulations are recorded below. The data indicate effectiveness of efforts to prevent predation on clams surviving the first year's plantings.

Methods

Details of the experimental design were presented in the previous paper (Kraeuter and Castagna 1977) and are briefly discussed below.

Four contiguous intertidal sites were marked by pushing stakes into the muddy substrate and two of the four sites were enclosed by 10 mm mesh plastic net 2.3 m high stretched around the 38 m circumference. The two remaining sites were left open (Figure 1). Crab traps were placed within one of the penned and one of the unpenned (no net) sites to assess the predatory effects of the blue crab, *Callinectes sapidus*. In addition, within each site, areas to be seeded were marked and designated to be treated with or without combinations of metal framed current baffles and crushed granite gravel. Current baffles 0.6 m high were constructed to decrease the scouring effects of currents. Since average tidal amplitudes are 1.2 m, the baffles did not prevent entrance of fish or crabs into the plots. Each baffle was about 1.5 m long and 12 baffles were set in an array forming four squares (Figure 1). Clam seed (about 2 mm) was planted in all sites at 3,000/m^2.

Clams were sampled in each site with a 7.4 cm diameter corer. A 0.6 m^2 grid was placed over each treatment and 10 random samples were removed in July 1977. This is a continuation of the previous year's sampling. For final sampling (October-November 1977), all sites were harvested using a suction sampler with an attached mesh bag. Four quadrats corresponding to the squares formed by placing current baffles in squares were sampled as discrete units (Figure 1). Where no baffles were utilized for the treatment, squares were marked by stakes and sampled as though the baffles had been present. All clams removed from the plots were brought to the laboratory, counted, and the percent commercial size (1 in (25.4 mm) thick New York legal limit) was determined. The data (counts) were transformed by $\log_{10}$ and compared by a factorial analysis of variance design (ANOVA).

Results and Discussion

Results from the first year sampling (through September 1976) indicated that baffles and gravel in combination were superior to any other treatment. Plots were sited in an area where predaceous echinoderms were not present, and although pens were not effective in preventing crab predation, no discernable damage could be attributed to other predators (Kraeuter and Castagna 1977).

The statistical summaries (Table 1) are a continuation of the table presented by Kraeuter and Castagna (1977), and, as in that paper, it is important to emphasize that the sampling results from one period to the next were not independent. The final data represent the cumulative effects of all environmental and biotic interactions on clams planted in fall 1975.

The July 1977 results mirrored those of earlier sampling periods (Kraeuter and Castagna 1977) with the exception that the pen × trap and pen × baffle × trap interactions were significant at the 0.05 level. This was due, in part, to the higher level of predation in the penned area without traps (18

[1]Contribution No. 924 from Virginia Institute of Marine Science.

[2]J. H. Lewis, seafood shipper and packer, Saxis, VA 23427, pers. commun. Nov. 1976.

[3]L. L. Burton, seafood shipper and packer, Burton's Seafood, Chincoteague, VA 23336, pers. commun. Sept. 1976.

[4]Merriner, J. V., and J. W. Smith. 1979. Gear feasibility study for the cownose ray, *Rhinoptera bonasus*. Va. Inst. Mar. Sci., Spec. Rep. Appl. Mar. Sci. Ocean Eng. 227, 27 p.

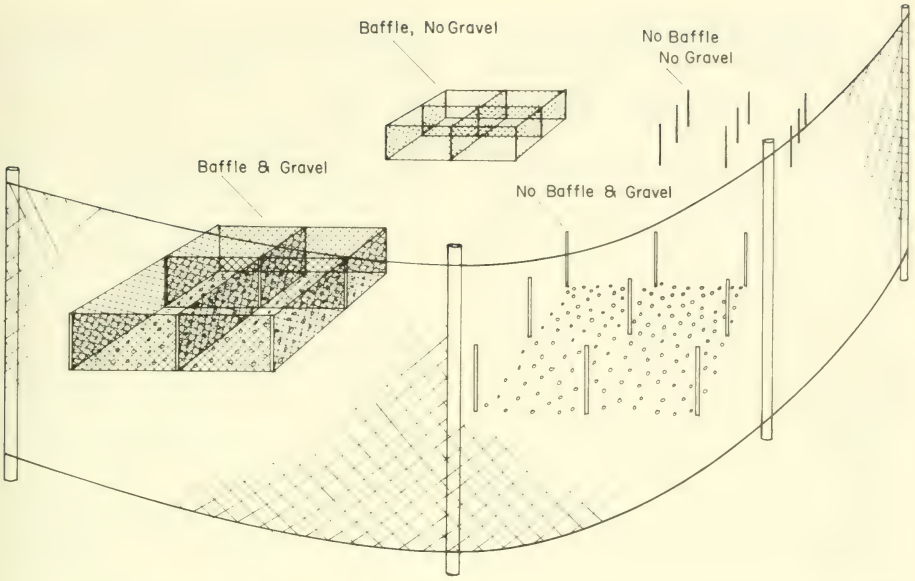


FIGURE 1.—Diagram of one site of the experimental design indicating the presence of each plot and the net for protection of juvenile *Mercenaria mercenaria*. Included in one site with a net would be a crab trap (not illustrated). The net was pushed into the substrate.

TABLE 1.—ANOVA table for survival of hard clam, *Mercenaria mercenaria*, juveniles with tests of pens, baffles, gravel, and traps and their interactions. Identical SS in the July data were caused by clams being absent in all sites with no baffle and no gravel.

	July 1977				October-November 1977			
Source of variation	df	SS	MS	*F*	df	SS	MS	*F*
Total	159	7.91			63	54.64		
Pens (P)	1	.02	0.02		1	4.31	4.31	114.31***
Baffles (B)	1	1.44	1.44	63.17***	1	32.17	32.17	853.37***
Gravel (G)	1	1.56	1.56	68.27***	1	10.21	10.21	270.89***
Traps (T)	1	.01	.01		1	.39	.39	10.43**
P × B	1	.05	.05		1	1.16	1.16	30.64***
P × G	1	.03	.03		1	2.76	2.76	73.30***
P × T	1	.09	.09	4.08*	1	.94	.94	24.90***
B × G	1	1.12	1.12	49.02***	1	07	.07	
B × T	1	.00	.00		1	.01	.01	
G × T	1	.001	.001		1	.42	.42	11.12**
P × B × G	1	08	.08		1	.04	.04	
P × B × T	1	.09	.09	4.05*	1	.001	.001	
P × G × T	1	07	.07		1	.01	.01	
B × G × T	1	.004	.004		1	.17	.17	4.61*
P × B × G × T	1	.07	.07		1	.16	.16	4.20*
Residual	144	3.29	.02		48	1.81	0.04	

***$P<0.001$, **$P<0.01$, *$P<0.05$.

clams sampled vs. 31 clams sampled in penned areas with traps), and, in part, to predation at the no pen no trap site, 23 clams sampled vs. 15 clams at the no pen plus trap site. These data indicate that trapping is essential in penned areas, but that when pens are absent crab trapping is of no benefit.

Within 2 wk following the July sampling, inspection of the sites revealed that clams 1.5-4.0 cm high had been crushed. These shell fragments

were the result of large predators. The shells were clean and some were mixed within the surface layer on the bottom. In addition, the predators had created pits 50 cm in diameter and 6-10 cm deep in the aggregate and substrate which had been covering the clams.

To eliminate effects of losses due to predation during the first year's study and concentrate on the effects due to these predators, we have utilized the estimate of the mean number of clams from the July 1977 samples as 100% of those present for further predation. The estimated numbers of clams in each experimental plot for July 1977 are given in Table 2, and the number of clams remaining for the corresponding treatments from the October to November 1977 sampling are given in the same table. Several important aspects not evident from the ANOVA table are apparent. A combination of baffles, gravel, pens, and traps was essential for high survival. Pens were significant only because of the predation between July and October. The percentage survival between these two sampling periods seemed to indicate that gravel somehow negatively interacted with the baffles (compare percent survival B + G and B + NG, Table 2) when pens were absent. This was not the case, but resulted from heavy predation in the baffle + gravel sites with no pens. Since there were more clams in these areas in July, the percent survival was lower, but total survival was better than in the baffle + no gravel sites (Table 2). The higher survival in the baffled sites was due to the protection the baffles offered the clams when the predators entered the area. Almost all clams found in these areas were close to, or beneath, the cross rods supporting the bottom of the baffle. This same shadow effect was the cause of the nonsignificant baffle + gravel interaction in the October-November ANOVA table. If more clams had been present in the B + NG sites, the clams would have been in the center of the plot and thus vulnerable to predation.

The impact of predation to the mariculture of clams can be seen by comparing survival inside and outside the penned sites (Table 2). Estimated survival inside a penned area was always more than 76%, and the average survival for both penned sites was 94% from July to October-November. Average survival for the same period in the unpenned sites was 8.75%. The greatest survival in the unpenned areas was 65% but, as explained above, was due to protection provided by baffle frames. These data indicate that at least 85-90% of the observed losses in the unpenned sites were due to predation. The importance of these data is amplified when the size of the clams is considered.

The average size of clams in July 1977 was 3.2 cm and by October was 3.9 cm (hinge to lip). The percentage marketable clams (1 in (25.4 mm) thick) was the same for both the penned and unpenned sites (58.5 and 58.6%) in October. This indicates no size selection of clams, but that clams of all sizes were consumed. The loss of such large clams represents 2 yr of work and a product of market size.

Flounders, known to prey on young *Mercenaria mercenaria* and to selectively eat the neck of adult clams, have been eliminated as potential predators because they are not capable of crushing the shell of 3 cm high hard clams. Of the seven species of fish capable of forming pits and crushing the shell of 3 cm size hard clams (Table 3), only two are known to be common away from the inlets and near the planted areas (Richards and Castagna 1970; Musick 1972). These two species, *Dasyatis centroura* and *Rhinoptera bonasus*, are prime suspects for causing the destruction in our unprotected plots. The former cannot be eliminated be-

TABLE 2.—Total number of clams estimated from mean number per sample (July 1977), total counts (October-November 1977), and the percent mortality between the sampling dates. — = not calculated because of 0 estimate in July. P = pens, T = traps, G = gravel, B = baffle. The prefix N = absence; NP = no pen, etc.

Month or period	Item	B · G	NB · G	B · NG	NBNG
July 1977	P + T	6,670	230	230	0
	P + NT	4,140	0	0	0
	NP + T	2,760	460	230	0
	NPNT	4,830	230	230	0
Oct.-Nov. 1977	P + T	6,723	174	352	2
	P + NT	3,228	23	126	2
	NP + T	257	17	75	2
	NPNT	248	13	148	5
% survival	P + T	101	76	153	—
July to Oct.-Nov.	P + NT	78	—	—	—
	NP + T	9	4	33	—
	NPNT	5	6	65	—

TABLE 3.—Potential fish predators on 3 cm hard clams in Virginia. Information from Richards and Castagna (1970) and Musick (1972).

Scientific name	Common name
Dasyatis americana	Southern stingray
D. centroura	Roughtail stingray
D. sayi	Bluntnose stingray
Myliobatis freminvillei	Bullnose ray
Aetobatus narinari	Spotted eagle ray
Rhinoptera bonasus	Cownose ray
Pogonias cromis	Black drum

cause of its large size and overall abundance within the area and the latter because of its schooling behavior. Schools of *R. bonasus* often destroy large areas of eelgrass and other habitats in search of clams, their primary food (Orth 1975, 1977). Burton (footnote 3) used hog wire fencing to keep schools of cownose rays from his beds of inventoried and replanted market size *Mercenaria*. Because of the suddenness of the disappearance (<2 wk) and the presence of crushed clam shell in this and other plantings, we believe the most likely predator was a school of *R. bonasus*.

Our data indicate that losses, due to such predation, would be unpredictable, but it would be financially devastating to the clam grower. The use of a fence or some other device to protect the clams is essential for successful field culture in areas where large predators occur. These fences can be removed during the winter to prevent ice damage, but along the Virginia coast they should be kept in place and maintained at all times from late March to early November.

Literature Cited

KRAEUTER, J. N., AND M. CASTAGNA.
1977. An analysis of gravel, pens, crab traps, and current baffles as protection for juvenile hard clams (*Mercenaria mercenaria*). Proc. 8th Annu. Meet. World Mariculture Soc., p. 581-592.

MUSICK, J. A.
1972. Fishes of Chesapeake Bay and the adjacent coastal plain. *In* M. L. Wass (compiler), A check list of the biota of lower Chesapeake Bay, p. 175-212. Va. Inst. Mar. Sci. Spec. Sci. Rep. 65.

ORTH, R. J.
1975. Destruction of eelgrass, *Zostera marina*, by the cownose ray, *Rhinoptera bonasus*, in the Chesapeake Bay. Chesapeake Sci. 16:205-208.
1977. The importance of sediment stability in seagrass communities. *In* B. C. Coull (editor), Ecology of marine benthos, p. 281-300. Belle W. Baruch Lib. Mar. Sci. 6. Univ. S.C. Press, Columbia.

RICHARDS, C. E., AND M. CASTAGNA.
1970. Marine fishes of Virginia's Eastern Shore (inlet and marsh, seaside waters). Chesapeake Sci. 11:235-248.

TILLER, R. E., J. B. GLUDE, AND L. D. STRINGER.
1952. Hard-clam fishery of the Atlantic coast. Commer. Fish. Rev. 14(10):1-25.

JOHN N. KRAEUTER
MICHAEL CASTAGNA

Virginia Insititute of Marine Science and
School of Marine Science
College of William and Mary
Wachapreague, VA 23480

A DIRECT METHOD FOR ESTIMATING NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, SPAWNING BIOMASS

Two methods exist for estimating spawning biomass, the total weight of mature fish, from abundance of spawning products. The first, or direct, method (Saville 1963) consists of dividing an estimate of egg production by the product of batch fecundity and the proportion of females in the mature stock. Saville safely assumed spawning frequency to be unity. The second method is indirect (Murphy 1966; Smith 1972) and utilizes information from two different species. Smith illustrated the second method, using information on the Pacific sardine, *Sardinops caerulea*, and northern anchovy, *Engraulis mordax*. Sardine spawner biomass is estimated from landings data and cohort analysis; anchovy spawner biomass is estimated by multiplying the estimated sardine spawner biomass by the product of the anchovy-to-sardine ratio of larval abundance and the sardine-to-anchovy ratios of fecundity, and spawning frequency. Computation was facilitated by assuming the unknown spawning frequencies to be equal, making the ratio of spawning frequencies unity. Up to the present only the second method has been used for the northern anchovy. This paper presents estimates derived from the first.

Computation of spawning biomass is simplified for the direct method when spawning occurs but once and for the indirect method when both species spawn with equal frequency. Difficulties arise when spawning is continuous and when it cannot be safely assumed that all mature fish spawn with the same frequency. This is the case with the northern anchovy. Spawning products are present all year, with a maximum abundance occurring in the late winter and early spring and a minimum during late summer and early fall. Abundance of and seasonal pattern of spawning products give no clue as to the number of spawnings by size and age, or even to the average number of spawnings.

Under the following conditions spawning frequency can be estimated from examining the spawning condition of females: 1) females can be examined for a characteristic that indicates when spawning takes place; 2) the length of time such a characteristic remains detectable can be estimated; 3) the spawning rate remains relatively constant over the sampling interval.

The spawning fraction, or frequency, is the

fraction of females displaying the characteristic divided by the length of the time interval the characteristic remains detectable. Say, from a sample of 10 females, 2 display a characteristic which lasts for 1 day and which indicates that spawning will take place in approximately 1 wk. The daily spawning fraction 1 wk hence will be 1/5.

Given this method for estimating spawning fraction the following relationship holds:

$$P = S(abc) \quad (1)$$

where P = production in eggs,
a = batch fecundity in (eggs)/(unit weight),
b = fraction spawning (weight of spawning females)/(weight of all mature females),
c = (weight of females)/(weight of spawning stock),
S = spawning biomass.

Spawning biomass can be estimated directly:

$$S = P(abc)^{-1}. \quad (2)$$

Hunter and Goldberg (1979) examined female northern anchovies for characteristics that would indicate a recent spawning. They found that following spawning follicles of the northern anchovy go through a sequence of identifiable degenerative stages. The first two stages, which Hunter and Goldberg referred to as day 0 and day 1, have durations of 1 day. Stage identification is subject to error. Day-0 follicles can be misidentified as day 1; day-1 follicles can be misidentified as day 2 and beyond. The most easily identified stage is day 1. If the spawning fraction, b, is based on day-1 follicles an adjustment factor, say d, is required in Equation (2):

$$S = P(ab'c)^{-1}d \quad (3)$$

where b', replacing b, is the observed fraction.

The adjustment factor is computed by using information on the fraction of day-0 follicles misclassified as day 1, say d_0, and the fraction of day-1 follicles correctly classified, say d_1.

$$d = (d_0 + d_1)$$
$$\mathrm{Var}(d) = \mathrm{Var}(d_0) + \mathrm{Var}(d_1).$$

Estimates based on Hunter and Goldberg's (1979, table 1) blind classification study for d_0 and d_1 are 5/21 and 16/19 respectively; hence

$$d = 1.080$$
$$\mathrm{Var}(d) = 0.016.$$

From examination of 195 females taken by midwater trawl during the time interval 15-27 February 1978, Hunter and Goldberg estimated the observed daily spawning fraction and its variance:

$$b' = 0.159$$
$$\mathrm{Var}(b') = 4.561 \times 10^{-4}.$$

Based on the total female weight of nonspawners the estimated batch fecundity and variance are from Hunter and Goldberg (1979, table 6)

$$a = 396 \text{ eggs/g (or } 3.96 \times 10^8 \text{ eggs/t)}$$
$$\mathrm{Var}(a) = 886.$$

For the time period 18 February-17 March 1978, Zweifel[1] estimated daily egg production. From 177 plankton samples, northern anchovy eggs and larvae were staged from time of spawning. Estimated total numbers at stage were regressed on time. The ordinate intercept, number at time zero, is the estimated egg production:

$$P = 2.321 \times 10^{13} \text{ eggs/d}$$
$$\mathrm{Var}(P) = 1.825 \times 10^{26}.$$

If the female to male sex ratio in numbers were 1:1 and if the two sexes had equal growth rates in terms of weight then c could be assumed to be 0.5. However, because of conflicting and insufficient evidence neither of these two hypotheses can be supported. Klingbeil (1978) demonstrated that the distribution of northern anchovy sexes is heterogeneous over space and time and that estimates of sex ratio are dependent on the sampling gear. From the purse seine fishery Klingbeil estimated that the ratio of numbers of females to males varies between 1.14:1 and 2.02:1 for 1969-76. From 9 yr of midwater trawl data Klingbeil estimated that the sex ratio is 1.03:1. Since midwater trawl surveys cover a wider geographic area and size range of anchovies, they probably provide an estimate closer to that of the true population sex ratio. However, since neither midwater trawl surveys

[1]James Zweifel, Southwest Fisheries Center La Jolla Laboratory, NMFS, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun.

nor purse seines are designed to estimate sex ratio it can only be stated that the anchovy sex ratio has not been adequately estimated.

Collins (1969) showed that females are greater in length and weight at age than males. However, since Collins' estimates are based on combined data from three fishing seasons and, since female weights are known to fluctuate within season due to spawning activity, the precision with which the data can be used for estimation purposes is open to speculation.

For the present purpose of estimating c the sex ratio of the number of females to males plus females as estimated from the February 1978 midwater trawl survey (Hunter and Goldberg 1979) will be used. Reexamining original data used by Hunter and Goldberg (1979, table 5) the ratio estimate is

$$\begin{aligned} c &= 0.550 \\ \mathrm{Var}(c) &= 0.001. \end{aligned}$$

This assumes, of course, an equal weight at age.

In the future, the best estimate of c is likely to be the ratio of the actual sampled weights of males and females; these were not available for the February 1978 survey. This would, of course, require the assumption that the sex ratio can differ from 1:1, that the weight distribution of the two sexes can change with time, and that a sample estimate is a better estimate than any hypothesized or long-term average value.

Using the following estimates

$$\begin{aligned} P &= 2.321 \times 10^{13} \text{ eggs/d} & c &= 0.550 \\ a &= 3.96 \times 10^{8} \text{ eggs/t} & d &= 1.080 \\ b' &= 0.159 \end{aligned}$$

the estimated S is approximately 0.72 million t. This is reasonably close to the estimate by the Smith procedure (Stauffer and Parker[2]) of 1.17 t.

At this time caution should be exercised in interpreting the general range described by these two estimates. The parameters of Smith's procedure have not been formally estimated. The parameter estimates of this new method are only first approximations. P may not be constant for as long a time interval as assumed here. Observed b' was found to be consistent for time of day, weight of fish, and geographic location. This may not prove to be the case under more intensive sampling. Another problem in estimating the spawning fraction is in determining female sexual maturity. This problem may be particularly acute for recently spawned young females where microscopic analysis is necessary to separate the recently spawned from the sexually immature. Misclassifying recently spawned as immature would tend to inflate the estimated b.

By the delta method (Seber 1973), the variance of S is

$$\mathrm{Var}(S) = (ab'c)^2 \left[d^2\mathrm{Var}(P) + P^2\mathrm{Var}(d) + (Pd)^2 \left[\frac{\mathrm{Var}(a)}{a^2} + \frac{\mathrm{Var}(b')}{b'^2} + \frac{\mathrm{Var}(c)}{C^2} \right] \right]. \quad (4)$$

Dividing Equation (4) by the square of Equation (3) and then taking the square root we have the coefficient of variation (CV) of spawning biomass

$$\mathrm{CV}(S) = \sqrt{[\mathrm{CV}(P)]^2 + [\mathrm{CV}(a)]^2 + [\mathrm{CV}(b)]^2 + [\mathrm{CV}(c)]^2 + [\mathrm{CV}(d)]^2}, \quad (5)$$

which is the component vector of the coefficients of variation of the estimated parameters, right side of Equation (3). Since possible covariance terms are neglected, Equation (5) may be somewhat oversimplified. However, Equation (5) allows a first approximation to delegating the relative impact of the precision of the individual parameter estimates. The squared coefficients of variation are as follows:

$$\begin{aligned} [\mathrm{CV}(P)]^2 &= 0.339 & [\mathrm{CV}(c)]^2 &= 0.003 \\ [\mathrm{CV}(a)]^2 &= 0.005 & [\mathrm{CV}(d)]^2 &= 0.013. \\ [\mathrm{CV}(b)]^2 &= 0.018 \end{aligned}$$

Thus $\mathrm{CV}(S) = 0.614$. P contributes approximately 8 times more to the coefficient of variation of the spawner biomass estimate than all other parameters combined. In the future, additional effort will be allocated to estimating production.

The utility of the direct method, Equation (2), lies in the fact that all the parameters can be estimated. The same samples used for estimating b' can be used to estimate a and c. This can be done with 2 wk of midwater trawling. It is hoped

[2]Stauffer, G. S., and K. R. Parker. 1978. Estimate of the spawning biomass of the northern anchovy central subpopulation for the 1978-79 fishing season. U.S. Dep. Commer., NOAA, NMFS/SWFC Adm. Rep. LJ-78-9, 10 p.

that precise estimation of production can be done within 30 d by sampling for eggs; this goal seems attainable for the northern anchovy. Utilization of the method for other species seems feasible.

Literature Cited

COLLINS, R. A.
1969. Size and age composition of northern anchovies (*Engraulis mordax*) in the California anchovy reduction fishery for the 1965-66, 1966-67, and 1967-68 seasons. *In* the northern anchovy (*Engraulis mordax*) and its fishery 1965-1968, p. 56-74. Calif. Dep. Fish Game, Fish Bull. 147.

HUNTER, J. R., AND S. R. GOLDBERG.
1980. Spawning incidence and batch fecundity in northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 77: 641-652.

KLINGBEIL, R. A.
1978. Sex ratios of the northern anchovy, *Engraulis mordax*, off southern California. Calif. Fish Game 64:200-209.

MURPHY, G. I.
1966. Population biology of the Pacific sardine (*Sardinops caerulea*). Proc Calif. Acad. Sci., Ser. 4, 34:1-84.

SAVILLE, A.
1964. Estimation of the abundance of a fish stock from egg and larval surveys. *In* J. A. Gulland (editor), On the measurement of abundance of fish stocks, p. 164-170. Rapp. P.-V. Réun. Cons. Perm. Int. Explor. Mer 155.

SEBER, G. A. F.
1973. The estimation of animal abundance and related parameters. Hafner Press, N.Y., 506 p.

SMITH, P. E.
1972. The increase in spawning biomass of northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 70: 849-874.

KEITH PARKER

Southwest Fisheries Center La Jolla Laboratory
National Marine Fisheries Service, NOAA
P.O. Box 271
La Jolla, CA 92038

FOOD OF THE HARBOR SEAL, *PHOCA VITULINA RICHARDSI*, IN THE GULF OF ALASKA

The harbor seal, *Phoca vitulina richardsi* (Shaughnessy and Fay 1977), is the most abundant and widespread coastal pinniped in the Gulf of Alaska. Harbor seals occupy virtually all nearshore habitats, and individuals occasionally occur as far as 100 km offshore (Spalding 1964; Wahl 1977; Fiscus et al.[1]). Despite their abundance and ecological importance, little information is available on their diet in Alaskan waters. In the most extensive food study published to date, Imler and Sarber (1947) examined stomachs of 99 seals from southeastern Alaska and 67 from the Copper River Delta. Wilke (1957) presented information on the food of seven harbor seals collected from Amchitka Island in the western Aleutian Islands. Kenyon (1965) reported on the stomach contents of 11 harbor seals taken in the same location. Bishop (1967) commented on stomach contents of two seals from Aialik Bay and two from Tugidak Island. Virtually no information has been available on the food of harbor seals from the Gulf of Alaska.

The study area (Figure 1) included coastal Gulf of Alaska from Yakutat Bay to Sanak Island. The portion of Cook Inlet north of Kachemak and Kamishak Bays was not included. The study area was divided into seven subareas for data analysis: northeastern Gulf of Alaska, Copper River Delta, Prince William Sound, Kenai coast, Lower Cook Inlet, Kodiak, and Alaska Peninsula.

Selection of Valdez as terminus of the trans-Alaskan oil pipeline and planned outer continental shelf oil and gas lease sales were the principal motivating factors for conducting this research. Production and transport of crude oil appeared to have the potential for significant alteration of the marine biota (Evans and Rice 1974) thus influencing the abundance and composition of harbor seal prey species. Established commercial fisheries for salmon, *Oncorhynchus* spp.; Pacific herring, *Clupea h. harengus*; halibut, *Hippoglossus stenolepis*; king crab, *Paralithodes camtschatica*; snow crab, *Chionoecetes bairdi*; Dungeness crab, *Cancer magister*; and shrimp, *Pandalus* spp., occur over the area, and pinnipeds are sometimes considered to be significant competitors with these fisheries. Data are needed to establish the possible impact of harbor seals on these commercially exploited species. Plans for developing fisheries are required by Federal laws (Public Law 94-265, Fishery Conservation and Management Act of 1976, and Public Law 92-522, Marine Mammal Protection Act of 1972) to utilize an integrated ecosystem approach to management

[1]Fiscus, C. H., H. W. Braham, R. W. Mercer, R. D. Everitt, B. D. Krogman, P. D. McGuire, C. E. Peterson, R. M. Sonntag, and D. E. Withrow. 1976. Seasonal distribution and relative abundance of marine mammals in the Gulf of Alaska. *In* Environmental assessment of the Alaskan Continental Shelf. Vol. 1. Principal investigators reports for October-December 1976, p. 19-264. Environmental Research Laboratories, NOAA, Boulder, Colo.

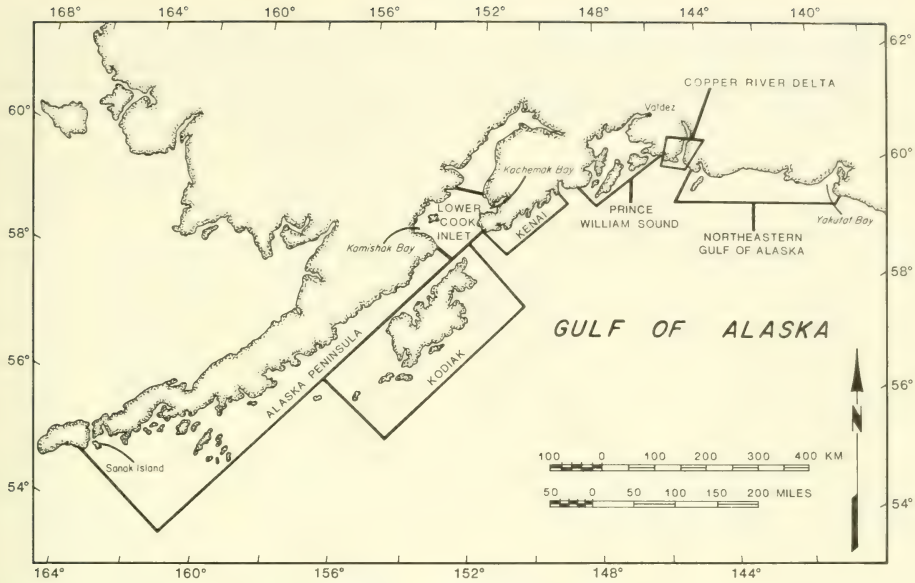


FIGURE 1.—Geographic subdivisions of Gulf of Alaska study area.

considering marine mammal populations as well as fishery resources.

Methods

A total of 548 harbor seals were collected by rifle throughout the Gulf of Alaska from 1973 through 1978 (Table 1). Reasonably complete seasonal coverage was obtained for Prince William Sound and the Kodiak area. Stomach contents were removed in the field, wrapped in muslin, and preserved in 10% Formalin.[2] In the laboratory the volumes and number of occurrences (number of stomachs in which a prey species was found) were determined for prey species. Because digestion was often advanced, skeletal materials, particularly fish otoliths and cephalopod mandibles (beaks), were the primary criteria for identification (Fitch and Brownell 1968; Pinkas et al. 1971).

Otoliths and other skeletal components from fish were tentatively identified to the lowest taxonomic level possible by comparison with reference materials. Otolith identifications were verified by John E. Fitch, California Department of Fish and Game, Long Beach. Cephalopod beaks were classified as either squid or octopus with the aid of Pinkas et al. (1971), and squid beaks were identified to family by Clifford H. Fiscus, National Marine Fisheries Service, NOAA, Seattle, Wash. Decapod crustaceans were identified by Kathryn J. Frost and Lloyd F. Lowry, Alaska Department of Fish and Game, Fairbanks.

In order to integrate data on both frequency of occurrence and prey volumes into a single ranking of prey utilization I used a modified form of the Index of Relative Importance (IRI)[3] devised by

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Geographic and seasonal distribution of harbor seals collected in the Gulf of Alaska.

Area	Number of seals			
	Jan.-Mar.	Apr.-June	July-Sept.	Oct.-Dec.
Northeastern Gulf of Alaska	—	22	—	9
Copper River Delta	—	18	27	—
Prince William Sound	62	24	26	39
Kenai coast	43	14	—	3
Lower Cook Inlet	—	37	—	—
Kodiak	4	106	38	53
Alaska Peninsula	—	20	3	—

[3]Original Index of Relative Importance as derived by Pinkas et al. (1971) was calculated by summing the numerical and volumetric percentage values and multiplying by the frequency of occurrence percentage value.

Pinkas et al. (1971). The numerical component of their formula was deleted because of the disparity in size of harbor seal prey items. The modified IRI was calculated as percentage of occurrences multiplied by percentage of volume.

Results

Food was present in 269 of the 548 stomachs. Fishes composed 74.5%, cephalopods 21.5%, and decapod crustaceans 4.0% of the occurrences (Table 2). A minimum of 27 species of fish were identified belonging to 13 families. Cephalopods included both octopus and squids of the family Gonatidae. Decapod crustaceans were primarily shrimps with one occurrence of a crab. The five top-ranked prey of harbor seals in the Gulf of Alaska were walleye pollock, octopus, capelin, eulachon, and Pacific herring (Table 3).

Regarding prey utilization by area of collection (Table 4), sample sizes were small and collections did not span all seasons (Table 1). Either walleye pollock or octopus was the top-ranked food in all marine areas and eulachon was dominant in the estuarian and freshwater habitats of the Copper River Delta. Walleye pollock was the top-ranked item in the eastern areas: northeastern Gulf of Alaska, Prince William Sound, and the Kenai coast. In the western areas: Lower Cook Inlet, Kodiak, and the Alaska Peninsula, octopus had the highest ranking. In Lower Cook Inlet, octopus and shrimps made up over 60% of both total

TABLE 2.—Stomach contents of 269 harbor seals collected in the Gulf of Alaska, all areas and seasons combined. [% under Occurrences = Percentage of occurrences and 95% confidence limits.]

Prey	Occurrences		Volume	
	No.	%	ml	%
Cephalopoda:	97	21.5±3.9	20,433	20.0
Octopus sp., octopus	77	17.1±3.5	18,753	18.3
Gonatidae, squids	20	4.4±2.0	1,680	1.6
Decapoda:	18	4.0±1.9	3,800	3.7
Shrimps	17	3.8±1.9	3,400	3.3
Crabs	1	0.2±0.5	400	0.4
Rajidae:				
Raja spp., skates	3	0.7±0.9	2,780	2.7
Clupeidae:				
Clupea h. harengus, Pacific herring	29	6.4±2.4	6,560	6.4
Salmonidae:				
Oncorhynchus spp., salmon	9	2.0±1.4	4,477	4.4
Osmeridae:	67	14.9±3.4	23,034	22.5
Mallotus villosus, capelin	40	8.8±2.7	10,687	10.4
Thaleichthys pacificus, eulachon	22	4.9±2.1	11,837	11.6
Hypomesus pretiosus, surf smelt	4	0.9±1.0	460	0.4
Unidentified Osmeridae, smelts	1	0.2±0.5	50	<0.1
Gadidae:	134	29.7±4.3	26,603	26.0
Eleginus gracilis, saffron cod	5	1.1±1.1	395	0.4
Gadus macrocephalus, Pacific cod	28	6.2±2.3	3,240	3.2
Microgradus proximus, Pacific tomcod	7	1.6±0.7	1,030	1.0
Theragra chalcogramma, walleye pollock	94	20.8±3.9	21,938	21.4
Zoarcidae:				
Lycodes spp., eelpouts	6	1.3±1.2	60	0.1
Scorpaenidae:				
Sebastes spp., rockfishes	4	0.9±1.0	810	0.8
Hexagrammidae:				
Hexagrammos spp., greenlings	2	0.4±0.7	400	0.4
Cottidae:	10	2.2±1.5	1,912	1.9
Dasycottus setiger, spinyhead sculpin	2	0.4±0.7	—	—
Enophrys bison, buffalo sculpin	1	0.2±0.5	240	0.2
Myoxocephalus spp., sculpins	2	0.4±0.7	1,430	1.4
Unidentified Cottidae, sculpins	5	1.1±1.1	242	0.2
Trichodontidae:				
Trichodon trichodon, Pacific sandfish	10	2.2±1.5	3,025	3.0
Bathymasteridae:				
Bathymaster signatus, searcher	3	0.7±0.9	40	<0.1
Ammodytidae:				
Ammodytes hexapterus, Pacific sand lance	19	4.2±2.0	463	0.5
Pleuronectidae:	23	5.3±2.2	2,615	2.6
Atheresthes stomias, arrowtooth flounder	3	0.7±0.9	—	—
Eopsetta jordani, petrale sole	1	0.2±0.5	—	—
Glyptocephalus zachirus, Rex sole	1	0.2±0.5	150	0.1
Hippoglossoides elassodon, flathead sole	5	1.1±1.1	130	0.1
Lepidopsetta bilineata, rock sole	1	0.2±0.5	—	—
Limanda aspera, yellowfin sole	6	1.3±1.2	1,650	1.6
Lyopsetta exilis, slender sole	2	0.4±0.7	—	—
Parophrys vetulus, English sole	2	0.4±0.7	65	<0.1
Unidentified Pleuronectidae	2	0.4±0.7	620	0.6
Unidentified fish remains	17	3.8±1.9	5,320	5.2
Totals	451	100.0	102,332	100.1

TABLE 3.—Rankings by modified Index of Relative Importance (IRI, see text footnote 3) of major prey of harbor seals collected in the Gulf of Alaska. Only those prey with IRI ≥2 are included.

Rank	Prey	Modified IRI	Occurrences (%)	Volume (%)
1	Walleye pollock	445	20.8	21.4
2	Octopus	313	17.1	18.3
3	Capelin	92	8.8	10.4
4	Eulachon	57	4.9	11.6
5	Pacific herring	41	6.4	6.4
6	Pacific cod	20	6.2	3.2
7.5	Flatfishes	13	5.1	2.6
7.5	Shrimps	13	3.8	3.3
9	Salmon	9	2.0	4.4
10	Squids	7	4.4	1.6
11	Pacific sandfish	7	2.2	3.0
12	Sculpins	4	2.2	1.9
14	Skates	2	0.7	2.7
14	Pacific sand lance	2	4.2	0.5
14	Pacific tomcod	2	1.6	1.0

TABLE 4.—Major prey of harbor seals from seven geographic areas in the Gulf of Alaska. Prey ranked in order of modified Index of Relative Importance (IRI, see text footnote 3). Only prey with IRI ≥2 are included. [Occurrences = Percentage of occurrences ± 95% confidence limits.]

Area and prey	IRI	Occurrences	Volume (%)
Northeastern Gulf of Alaska (stomachs with contents 17; occurrences 39; volume 2,420 ml)			
Walleye pollock	640	28.2±15.4	22.7
Surf smelt	196	10.3±10.8	19.0
Capelin	143	23.1±14.5	6.2
Shrimps	131	2.6± 6.3	50.4
Copper River Delta (stomachs with contents 14; occurrences 15; volume 8,115 ml)			
Eulachon	8,826	93.3±17.4	94.6
Salmon	36	6.7±17.4	5.4
Prince William Sound (stomachs with contents 83; occurrences 122; volume 28,290 ml)			
Walleye pollock	1,375	29.5± 8.5	46.6
Pacific herring	166	14.8± 6.7	11.2
Squids	77	13.1± 6.4	5.9
Octopus	75	13.9± 6.6	5.4
Salmon	33	3.3± 3.6	10.0
Capelin	16	4.1± 3.9	3.8
Pacific tomcod	5	1.6± 2.7	3.3
Pacific cod	4	4.9± 4.2	0.9
Saffron cod	3	2.5± 3.2	1.3
Eulachon	3	1.6± 2.7	1.9
Kenai coast (stomachs with contents 30; occurrences 52; volume 7,225 ml)			
Walleye pollock	1,503	40.4±14.3	37.2
Pacific herring	247	11.5± 9.6	21.5
Pacific sandfish	44	7.7± 8.2	5.7
Capelin	19	5.8± 7.3	3.3
Pacific tomcod	4	3.8± 6.2	1.0
Lower Cook Inlet (stomachs with contents 17; occurrences 23; volume 5,412 ml)			
Octopus	1,697	39.1±23.4	43.4
Eulachon	532	17.4±18.6	30.6
Shrimps	501	21.7±20.0	23.1
Capelin	17	8.7±14.4	1.9
Kodiak Island (stomachs with contents 102; occurrences 192; volume 42,685 ml)			
Octopus	631	21.4± 6.1	29.5
Capelin	323	10.9± 4.7	21.3
Walleye pollock	70	12.0± 4.9	5.8
Flatfishes	63	10.9± 4.7	5.8
Pacific cod	55	8.3± 4.2	6.6
Pacific sand lance	9	8.3± 4.2	1.1
Pacific herring	9	2.1± 2.3	4.2
Shrimps	8	3.6± 2.9	2.2
Salmon	6	2.1± 2.3	2.9
Sculpins	3	4.2± 3.1	0.7
Eulachon	2	0.5± 1.3	4.6
Alaska Peninsula (stomachs with contents 6; occurrences 9; volumes 8,185 ml)			
Octopus	929	33.3±41.8	27.9
Walleye pollock	824	22.2±37.5	37.1
Pacific sandfish	342	11.1±29.7	30.8
Pacific cod	40	22.2±37.5	1.8
Sculpins	26	11.1±29.7	2.3

occurrences and volumes which was nearly twice the percentages in other areas.

Chi-square analyses of prey occurrences for Kodiak Island and Prince William Sound indicated that in Prince William Sound more walleye pollock ($P<0.01$) were eaten than in Kodiak (Table 5). In Kodiak there was higher utilization ($P<0.05$) of capelin than in Prince William Sound. Octopus and Pacific cod were not utilized at significantly different rates ($P>0.05$). While samples were inadequate for statistical testing, it appeared that more squids and Pacific herring and fewer Pacific sand lances, flatfishes, and sculpins were eaten in Prince William Sound than in Kodiak.

TABLE 5.—Comparison of occurrences of principal prey ($N\geq4$) of harbor seals collected in Prince William Sound and the Kodiak Island area. Statistical comparisons were made by chi-square analysis. [% = Percentage ± 95% confidence limits; — = Inadequate sample for statistical testing.]

	Kodiak		Prince William Sound		
Prey	No.	%	No.	%	P
Octopus	41	21.4±6.1	17	13.9±6.5	>0.05
Squids	2	1.0±1.7	16	13.1±6.4	—
Shrimps	7	3.6±2.9	1	0.8±2.0	—
Pacific herring	4	2.1±2.3	18	14.8±6.7	—
Salmon	4	2.1±2.3	4	3.3±3.6	—
Capelin	21	10.9±4.7	5	4.1±3.9	<0.05
Pacific cod	16	8.3±4.2	6	4.9±4.2	>0.10
Walleye pollock	23	12.0±4.9	36	29.5±8.5	<0.01
Sculpins	8	4.2±3.1	0	0.0	—
Pacific sand lance	16	8.3±4.2	0	0.0	—
Flatfishes	21	10.9±4.7	1	0.8±2.0	—
Total occurrences	192		122		

Salmon were found in the diet of harbor seals from both Prince William Sound and the Kodiak Island area only during the summer (Table 6). In the Kodiak area, feeding on Pacific sand lance appeared to be greatest in the fall while use of capelin seemed to peak in the spring. Use of Pacific herring by harbor seals appeared greatest in the spring in Prince William Sound.

Prey items were found in the stomachs of 13 harbor seal pups 2.5-11 mo of age and included shrimps, capelin, Pacific tomcod, walleye pollock, and Pacific sand lance. All items were <15 cm total length.

Discussion

The high ranking of walleye pollock in the harbor seal diet may have been a direct function of its abundance. Pereyra and Ronholt[4] found that walleye pollock was the dominant fish species in the Gulf of Alaska, composing 45% by weight of total fish stocks. Octopus, the second-ranked prey, appears to be an important food of harbor seals throughout the eastern North Pacific as nearly all food studies have found them to be a major component of the diet (Scheffer and Sperry 1931; Imler and Sarber 1947; Fisher 1952; Wilke 1957; Spalding 1964; Kenyon 1965; Bishop 1967). Five of the six, top-ranked prey were off-bottom, schooling fishes. Use of this type of prey may minimize

[4]Pereyra, W. T., and L. L. Ronholt. 1976. Baseline studies of demersal resources of the northern Gulf of Alaska shelf and slope. U.S. Dep. Commer., NOAA Processed Rep. NMFS NWFC, 281 p.

TABLE 6.—Seasonal occurrences of principal prey ($N \geq 4$) of harbor seals from the Kodiak Island area and Prince William Sound. [No. = Occurrences of prey; % = Percentage and 95% confidence limits.]

Area and prey	Jan.-Mar.		Apr.-June		July-Sept.		Oct.-Dec.	
	No.	%	No.	%	No.	%	No.	%
Kodiak Island area:								
Octopus	0	0.0	24	25.8± 9.4	6	15.0±12.3	9	15.8±10.3
Salmon	0	0.0	0	0.0	4	10.0±10.5	0	0.0
Capelin	0	0.0	14	15.1± 7.8	3	7.5± 9.4	3	5.3± 6.7
Pacific cod	0	0.0	8	8.6± 6.2	3	7.5± 9.4	4	7.0± 7.5
Walleye pollock	0	0.0	15	16.1± 8.0	3	7.5± 9.4	6	10.5± 8.8
Pacific sand lance	0	0.0	0	0.0	3	7.5± 9.4	12	21.1±11.5
Total occurrences	2		93		40		57	
Prince William Sound:								
Octopus	9	15.8±10.3	2	15.4±21.6	2	14.3±20.1	5	13.2±12.1
Squids	8	14.0± 9.9	0	0.0	3	21.4±23.5	5	13.2±12.1
Herring	8	14.0± 9.9	5	38.5±29.2	2	14.3±20.1	2	5.3± 8.4
Salmon	0	0.0	0	0.0	4	28.6±25.9	0	0.0
Capelin	4	7.0± 7.5	0	0.0	1	7.1±14.7	0	0.0
Walleye pollock	15	26.3±12.3	4	30.8±27.7	1	7.1±14.7	15	39.5±16.9
Total occurrences	57		13		14		38	

foraging effort and conserve energy compared with selection of more solitary species (Smith and Gaskin 1974).

The major differences in prey utilization between Prince William Sound and Kodiak are not readily explainable. However, water depths and topography for the two areas are considerably different (U.S. Department of Commerce[5]). Kodiak waters have considerable shallow shelf area, particularly east and south of the Island, and Prince William Sound generally has a rocky, precipitous coast and deep waters reaching 740 m. These features may influence prey composition, abundance, and availability to harbor seals.

Differential utilization of certain prey by season appeared to be explained by availability in most instances. Salmon occurred in stomachs of seals from both Kodiak and Prince William Sound only during the summer. In both areas salmon are only available in quantity in nearshore waters during this period. The apparent increases during spring in utilization of herring in Prince William Sound and capelin in the Kodiak area probably reflected nearshore distribution associated with spawning in these species (Hart 1973; Jangaard 1974). In the Kodiak area, Pacific sand lance were utilized to a greater extent during fall. No reason is known for this.

Six of the 10, top-ranked prey; walleye pollock, Pacific herring, Pacific cod, flatfishes, shrimps, and salmon are either currently harvested commercially or may be harvested in the near future (North Pacific Fishery Management Council[6]). Of particular interest is the possibility of increased harvests of walleye pollock which was the top-ranked prey of harbor seals accounting for about 21% of both total occurrences and volumes of food items. Sergeant (1976) believed that fisheries could compete with natural predators and cause their populations to stabilize at levels well below those existing prior to the fishery.

Harbor seals are present on the Copper River Delta from May through September. The results of this study and those of Imler and Sarber (1947) indicated that eulachon was the dominant prey from late May to mid-July. Nothing is known about feeding during late summer and fall when eulachon are not present.

Although specialized feeding on shrimps by newly weaned harbor seal pups was reported by Havinga (1933), Fisher (1952), and Bigg (1973), small fishes were the primary food of young seals <1 yr old collected during this study.

During this study several sampling problems and prey identification biases became apparent. Distinct geographic and seasonal variations in prey utilization were found to occur and because of this it was difficult to determine if a completely representative sample was obtained. Also, our sampling was restricted to nearshore waters. If a significant amount of feeding took place offshore and availability and composition of potential prey was different there, the results of this study would not be totally representative. In addition, the probability of detecting and identifying various

[5]U.S. Department of Commerce, NOAA, Nautical Charts No. 8556 and 16700.

[6]North Pacific Fishery Management Council. 1978. Fishery management plan for the Gulf of Alaska groundfish fishery during 1978. Unpubl. manuscr., 220 p. North Pacific Fishery Management Council, P.O. Box 3136 DT, Anchorage, AK 99510.

prey in the stomachs was not equal. Cephalopod beaks are not always passed through the intestinal tract and may remain in the stomach for several days before they are regurgitated (Pitcher unpubl. data). This increases the probability of detection thereby exaggerating estimates of their utilization.

Acknowledgments

This study was supported in part by the Bureau of Land Management through an interagency agreement with the National Oceanic and Atmospheric Administration, under which a multiyear program responding to needs of petroleum development of the Alaska continental shelf is managed by the Outer Continental Shelf Environmental Assessment Program office. Support was also provided by the Marine Mammal Commission and the Alaska Department of Fish and Game. I am grateful to R. Aulabaugh, D. Calkins, D. McAllister, and K. Schneider for field assistance. Thanks are due to D. Calkins, F. Fay, K. Frost, L. Lowry, D. McKnight, and K. Schneider who reviewed drafts of this paper.

Literature Cited

BIGG, M. A.
1973. Adaptations in the breeding of the harbour seal, (*Phoca vitulina*). J. Reprod. Fert., Suppl. 19:131-142.

BISHOP, R. H.
1967. Reproduction, age determination and behavior of the harbor seal, (*Phoca vitulina*) in the Gulf of Alaska. M.S. Thesis, Univ. Alaska, College, 121 p.

EVANS, D. R., AND S. D. RICE.
1974. Effects of oil on marine ecosystems: A review for administrators and policy makers. Fish. Bull., U.S. 72:625-638.

FISHER, H. D.
1952. The status of the harbour seal in British Columbia, with particular reference to the Skeena River. Fish. Res. Board Can., Bull. 93, 58 p.

FITCH, J. E., AND R. L. BROWNELL, JR.
1968. Fish otoliths in cetacean stomachs and their importance in interpreting feeding habits. J. Fish. Res. Board Can. 25:2561-2574.

HART, J. L.
1973. Pacific fishes of Canada. Fish. Res. Board Can., Bull. 180, 740 p.

HAVINGA, B.
1933. Der Seehund in den Hollandischen Gerwassern. Tijdschr. Ned. Dierkd. Ver. 3:79-111.

IMLER, R. H., AND H. R. SARBER.
1947. Harbor seals and sea lions in Alaska. U.S. Fish Wildl. Serv., Spec. Sci. Rep. 28, 23 p.

JANGAARD, P. M.
1974. The capelin (*Mallotus villosus*) biology, distribution, exploitation, utilization, and composition. Fish. Res. Board Can., Bull. 186, 70 p.

KENYON, K. W.
1965. Food of harbor seals at Amchitka Island, Alaska. J. Mammal. 46:103-104.

PINKAS, L., M. S. OLIPHANT, AND I. L. K. IVERSON.
1971. Food habits of albacore, bluefin tuna, and bonito in California waters. Calif. Dep. Fish Game, Fish Bull. 152, 105 p.

SCHEFFER, T. H., AND C. C. SPERRY.
1931. Food habits of the Pacific harbor seal, *Phoca richardii*. J. Mammal. 12:214-226.

SERGEANT, D. E.
1976. History and present status of populations of harp and hooded seals. Biol. Conserv. 10:95-118.

SHAUGHNESSY, P. D., AND F. H. FAY.
1977. A review of the taxonomy and nomenclature of north Pacific harbour seals. J. Zool. (Lond.) 182:385-419.

SMITH, G. J. D., AND D. E. GASKIN.
1974. The diet of harbor porpoises (*Phocoena phocoena* (L.)) in coastal waters of Eastern Canada, with special reference to the Bay of Fundy. Can. J. Zool. 52:777-782.

SNEDECOR, G. W., AND W. G. COCHRAN.
1967. Statistical methods. 6th ed. Iowa State Univ. Press, Ames, 593 p.

SPALDING, D. J.
1964. Comparative feeding habits of the fur seal, sea lion, and harbour seal on the British Columbia coast. Fish. Res. Board Can., Bull. 146, 52 p.

WAHL, T. R.
1977. Sight records of some marine mammals offshore from Westport, Washington. Murrelet 58:21-23.

WILKE, F.
1957. Food of sea otters and harbor seals at Amchitka Island. J. Wildl. Manage. 21:241-242.

KENNETH W. PITCHER

Alaska Department of Fish and Game
333 Raspberry Road
Anchorage, AK 99502

PRODUCTION AND GROWTH OF SUBYEARLING COHO SALMON, *ONCORHYNCHUS KISUTCH*, CHINOOK SALMON, *ONCORHYNCHUS TSHAWYTSCHA*, AND STEELHEAD, SALMO GAIRDNERI, IN ORWELL BROOK, TRIBUTARY OF SALMON RIVER, NEW YORK

Decline of lake trout, *Salvelinus namaycush*, and burbot, *Lota lota*, populations in the Great Lakes from 1930 to 1950 created a void of a large offshore piscivore in these waters. Smith (1968) attributed the decline to overexploitation by the commerical fishery and predation by the sea lamprey, *Petromyzon marinus*. The decline was followed by proliferation of the alewife, *Alosa pseudoharengus*, in Lakes Ontario, Huron, and Michigan

(Berst and Spangler 1973; Christie 1973; Wells and McLain 1973). As a result the State of Michigan in 1966 undertook a program to establish coho salmon, *Oncorhynchus kisutch*, in Lakes Michigan and Superior in hopes of creating a valuable sport fishery based on alewife as the major forage species (Tody and Tanner[1]). The success of the Michigan program provided an incentive to other states and provinces bordering the Great Lakes to undertake similar programs.

New York State began its salmonid program for Lake Ontario in 1968 when 41,000 coho salmon were planted in the Salmon River. The following year 70,000 chinook salmon, *O. tshawytscha*, were planted in the Little Salmon River (Parsons 1973). Stocking of steelhead, *Salmo gairdneri*, commenced in 1974 (Parker[2]). Stockings of coho salmon and steelhead have continued annually since their inception. Chinook salmon plantings were stopped after releases in the spring of 1976 because contaminant levels in their flesh generally exceeded action levels for Mirex[3] and PCB's when these fish first became available to anglers as precocious jacks on their maiden spawning run at 1.8-2.7 kg (New York State Department of Environmental Conservation[4]). However, chinook salmon stocking was resumed in 1979.

From its inception, Michigan's salmonid program has given high priority to natural reproduction as a supplement to hatchery production (Tody and Tanner footnote 1). Subsequent studies have focused on the extent of natural reproduction in Michigan (Stauffer[5]) and other ecological aspects of spawning activity (Taube[6]). Reproductive success of Pacific salmonids has been examined in Minnesota (Hassinger et al. 1974) and Wisconsin (Avery[7]). Canadian studies on Great Lakes tributaries have mainly focused on steelhead reproduction (Alexander and MacCrimmon 1974).

In New York, chinook salmon begin their spawning run from Lake Ontario in late August and early September (Jolliff[8]). Chinook salmon redds are present as early as mid-September in the Salmon River in Oswego County. Although most chinook salmon spawning occurs in the Salmon River, smaller tributaries are also utilized. Spawning in smaller tributaries usually does not begin until late September with the peak occurring in mid-October. The selection of larger tributaries such as the Salmon River for spawning is characteristic of chinook salmon in their native range (Stein et al. 1972; Scott and Crossman 1973). Coho salmon run somewhat later than chinook salmon, usually beginning in late September and peaking in late October to early November. Limited coho salmon spawning activity occurs in the Salmon River, possibly because of the large size of the substrate materials. Adult steelhead are present in the Salmon River throughout the fall and into early summer. Steelhead can be found in the smaller tributaries from March through June with most spawning activity occurring in April and May. Stream residence time for juvenile salmonids in the Salmon River system is <1 yr for chinook salmon, up to 1 yr for coho salmon, and up to 2 yr for steelhead (Johnson 1978).

Prior to 1977 the reproductive success of Pacific salmonids was unknown in New York tributaries of Lake Ontario. In 1977, five streams in the Salmon River system were examined for evidence of successful spawning of coho salmon, chinook salmon, and steelhead (Johnson 1978). Initial evidence indicated substantial reproduction of coho salmon and steelhead in some of the streams. The purpose of this study was to quantify reproductive success of Pacific salmonids in one tributary of the Salmon River.

Methods

Orwell Brook was selected as it contained high densities of coho and chinook salmon and steelhead juveniles. Orwell Brook flows for ap-

[1]Tody, W. H., and H. A. Tanner. 1966. Coho salmon for the Great Lakes. Mich. Cons. Dep. Fish. Manage. Rep. 1, 38 p. Fish Division, Michigan Department of Natural Resources, Mason Building, Lansing, MI 48926.

[2]C. E. Parker, Chief, Bureau of Fisheries, New York State Department of Environmental Conservation, 50 Wolf Road, Albany, NY 12233, pers. commun. October 1979.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[4]New York State Department of Environmental Conservation. 1977. Monthly report on toxic substances impacting on fish and wildlife. Rep. 1, April 20, 1977.

[5]Stauffer, T. M. 1977. Numbers of juvenile salmonids produced in five Lake Superior tributaries and the effect of juvenile coho salmon on their numbers and growth, 1967-1974. Mich. Dep. Nat. Resour., Fish. Res. Rep. 1846, 29 p. Institute for Fisheries Research, Museums Annex Building, Ann Arbor, MI 48109.

[6]Taube, C. M. 1975. Abundance, growth, biomass, and interrelationship of trout and coho salmon in the Platte River. Mich. Dep. Nat. Resour., Fish. Res. Rep. 1830, 82 p. Institute for Fisheries Research, Museums Annex Building, Ann Arbor, MI 48109.

[7]Avery, E. L. 1974. Reproduction and recruitment of anadromous salmonids in Wisconsin tributaries of Lake Michigan. Dingell-Johnson final Rep., Proj. F-33-R, Study 108, Wis. Dep. Nat. Resour., 32 p.

[8]T. Jolliff, Associate Aquatic Biologist, Bureau of Fisheries, New York State Department of Environmental Conservation, Cape Vincent, NY 13618, pers. commun.

proximately 14.5 km before entering the Salmon River, 17 km from Lake Ontario (Figure 1). About 60% of Orwell Brook is considered adequate for successful salmonid reproduction with suitable substrate generally consisting of gravel (1-2 cm in diameter) and pebbles (3-6 cm in diameter). The maximum summer water temperature recorded during 1977 and 1978 was 21° C. Mean monthly stream discharge from June to October 1978 was 0.26 m^3/s. Salmonids, cyprinids, and catostomids, in order of abundance are the principal components of the Orwell Brook fish fauna.

A single 100 m station was established on Orwell Brook 3 km above the Salmon River. This section was generally characteristic of the lower portion of Orwell Brook. Sections of the stream were visually examined weekly from early May to mid-June in 1978 in order to estimate the approximate time of peak emergence of salmon fry. Peak emergence, as used in this study, occurred when the densities of coho and chinook salmon and steelhead were highest in Orwell Brook. Collections of juvenile salmonids were made monthly from May to October with a 3 m minnow seine. Supplemental observations on salmon emergence were also made in May 1979. Monthly population estimates derived using the Chapman mark-recapture index (Ricker 1975) and average monthly weights of juvenile salmonids were plotted with the area beneath the curve providing an estimate of total production (Chapman 1968). A logarithmic plot assuming an exponential decline in monthly densities was used to determine the population size at peak emergence for coho and chinook salmon. This method, based on the assumption that natural mortality is greatest just after emergence and then gradually diminishes, has previously been employed to estimate the

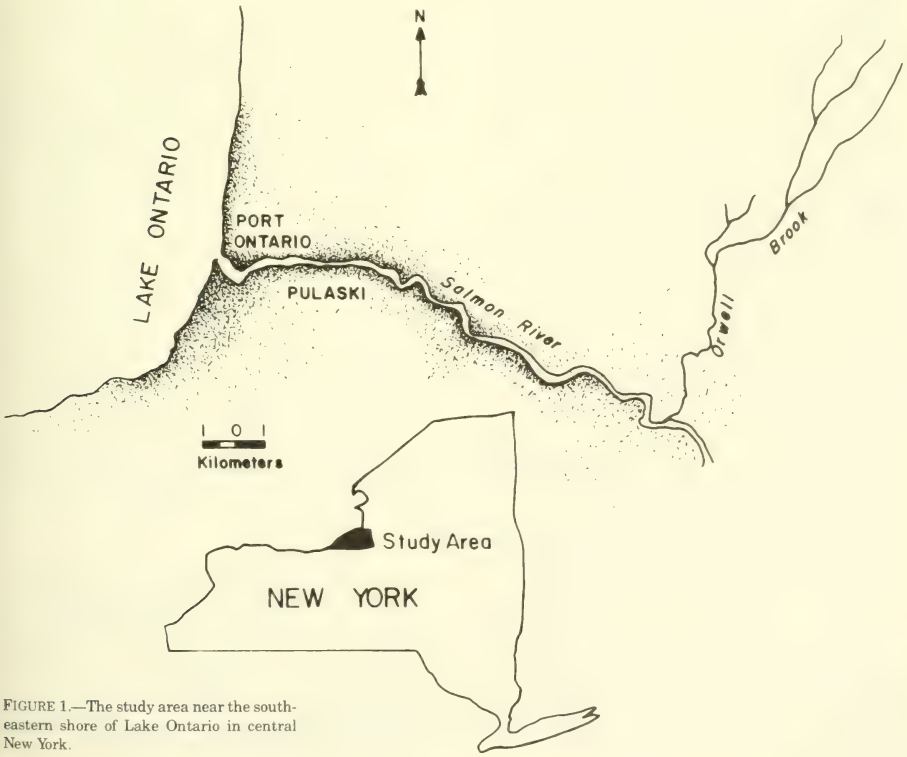


FIGURE 1.—The study area near the southeastern shore of Lake Ontario in central New York.

population size at peak emergence in salmonid populations (Hunt 1966; O'Connor and Power 1976). Total production of each species was divided by the smallest stream area within the 100 m section that was recorded during the study in order to give an estimate of production per unit area.

Results and Discussion

Recently emerged coho and chinook salmon were first observed in Orwell Brook in 1978 on May 13. In 1979, coho salmon were first observed on May 9th and chinook salmon on May 10. Peak emergence of both species occurred during early June 1978. Steelhead began emerging during mid-June and peaked in early to mid-July.

Population estimates were initiated in mid-June about 2 wk after peak salmon emergence. At this time both salmon species were abundant in the main stream and steelhead had started to emerge. Estimates of population size at peak emergence were 718 coho salmon and 189 chinook salmon fry/100 m in the section (Table 1). Densities of fry (number per square meter) at this time were 1.30 and 0.34 for coho and chinook salmon (Table 1). The initial estimate of steelhead in June was 103 fry/100 m or 0.20 fry/m^2 of stream bottom. However, the highest densities of steelhead fry were not recorded until August (Table 1).

Total production of subyearling coho salmon from 1 June to 30 October 1978 was 1,248 g. This was substantially greater than production of chinook salmon, 282 g and steelhead, 404 g (17 June-10 October) (Figure 2). Production per square meter was 2.7, 0.6, and 0.9 g for coho and chinook salmon and steelhead. Combined total production of the three species was 4.2 g/m^2 for the period of study.

Production of subyearling coho salmon in Orwell Brook during 1978 was intermediate between

TABLE 1.—Estimated monthly numbers (with 95% confidence limits) and densities (number per square meter) of subyearling coho salmon, chinook salmon, and steelhead in 100 m study area of Orwell Brook, Oswego County, N.Y., during 1978.

Date	Stream area (m^2)	Coho salmon		Chinook salmon		Steelhead	
		Number	Density	Number	Density	Number	Density
1 June	553	[1]718	1.30	[1]189	0.34	—	—
17 June	521	500±101	1.04	139±43	.27	103±41	0.20
16 July	483	428±184	.89	121±50	.25	212±72	.44
12 Aug.	469	118±64	.25	51±29	.11	262±84	.56
10 Sept.	476	104±62	.22	36±25	.08	199±58	.42
10 Oct.	495	68±23	.14	31±16	.06	138±34	.28

[1]Logarithmic extrapolation.

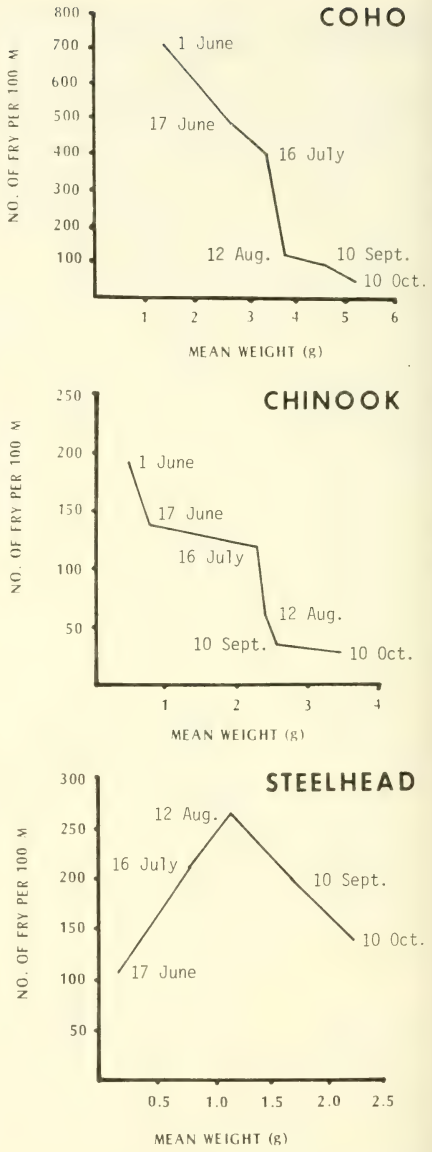


FIGURE 2.—Production curves of subyearling coho and chinook salmon in Orwell Brook, Oswego County, N.Y., 1 June-10 October 1978, and steelhead 17 June-10 October 1978.

that observed in Oregon, 5.6 g/m² (Chapman 1965) and Michigan, 0-1.9 g/m² (Stauffer[9]) during a similar time interval. Production of coho salmon in the 100 m section of Orwell Brook from 1 June to 15 October 1977 was 5.9 g/m² (Johnson 1978). Although the 1978 production estimate for coho salmon represents a 54% decrease from 1977, the variation in production between years is within the range reported by Chapman (1965) for coho salmon in Oregon coastal streams.

No information on chinook salmon production is available for the Great Lakes region; however, production of chinook salmon in Orwell Brook was intermediate to that recorded in the Lemhi River and Big Springs Creek, Idaho (Goodnight and Bjornn 1971). Production of steelhead is less than recorded in Michigan (Hannuksela[10]) and intermediate between the two Idaho streams (Goodnight and Bjornn 1971).

From emergence in May until the termination of sampling in November, subyearling coho salmon were larger than either subyearling chinook salmon or steelhead (Table 2). However, since chinook salmon characteristically leave their natal streams earlier than coho salmon, larger chinook salmon smolts may be migrating early. The growth rate (total length in millimeters per day) of coho and chinook salmon and steelhead was greatest during the first 2 mo following emergence (Table 2). Growth during this 2 mo period was 0.44, 0.47, and 0.39 mm/d for coho and chinook salmon and steelhead (Table 2). High initial growth rates of subyearling coho salmon and steelhead have previously been reported by Chapman (1965) and Stauffer (footnote 9). For the entire period (175 d for salmon, 145 d for steelhead) the growth rates of chinook salmon and steelhead were identical, 0.27 mm/d, with coho salmon being only slightly slower, 0.26 mm/d. In Michigan, growth rates of subyearling coho salmon and steelhead from June to November were 0.29 and 0.26 mm/d (Stauffer footnote 9). However, although these estimates are similar to those obtained in Orwell Brook, both coho salmon and steelhead are initially larger in June in Orwell Brook and this size differential (especially for coho salmon) is retained throughout the fall. There is no available information on chinook salmon growth in the Great Lakes region; however, growth in New York is slower than reported in Washington (Becker 1973).

TABLE 2.—Number examined, mean total length (millimeters) (with 95% confidence limits), and daily growth increments (mm/d) of subyearling coho salmon, chinook salmon, and steelhead from Orwell Brook, May-November 1978.

	Coho salmon			Chinook salmon			Steelhead		
Date	No.	$\overline{TL}$	mm/d	No.	$\overline{TL}$	mm/d	No.	$\overline{TL}$	mm/d
18 May	10	45.1±4.4		10	36.7±3.9				
			0.65			0.34			
17 June	20	63.6±5.7		20	46.7±1.9		10	29.7±1.8	
			0.26			0.61			0.52
16 July	40	71.1±2.8		40	64.5±2.0		30	44.9±1.6	
			0.13			0.06			0.24
12 Aug.	30	74.7±2.5		20	66.0±3.0		25	51.5±1.7	
			0.27			0.11			0.19
10 Sept.	20	82.4±4.9		20	69.2±3.0		30	57.0±3.2	
			0.05			0.22			0.16
10 Oct.	20	83.9±4.9		10	75.7±3.4		25	61.7±3.8	
			0.22			0.28			0.26
9 Nov.	10	90.4±5.2		10	84.0±4.3		10	69.5±4.1	

Acknowledgments

I wish to thank E. M. Zebisch for assistance in the field and J. D. Sheppard and E. W. Radle for reviewing preliminary drafts of the manuscript. The comments and suggestions of two anonymous reviewers substantially contributed to the content of the final manuscript.

Literature Cited

ALEXANDER, D. R., AND H. R. MACCRIMMON.
1974. Production and movement of juvenile rainbow trout (*Salmo gairdneri*) in a headwater of Bothwell's Creek, Georgian Bay, Canada. J. Fish. Res. Board Can. 31:117-121.

BECKER, C. D.
1973. Food and growth parameters of juvenile chinook salmon, *Oncorhynchus tshawytscha*, in central Columbia River. Fish. Bull.,'U.S. 71:387-400.

BERST, A. H., AND G. R. SPANGLER.
1973. Lake Huron: The ecology of the fish community and man's effects on it. Great Lakes Fish. Comm. Tech. Rep. 21, 41 p.

CHAPMAN, D. W.
1965. Net production of juvenile coho salmon in three Oregon streams. Trans. Am. Fish. Soc. 94:40-52.
1968. Production. *In* W. E. Ricker (editor), Methods for assessment of fish production in fresh waters, p. 182-196. Blackwell Sci. Publ., Oxf., Engl.

CHRISTIE, W. J.
1973. A review of the changes in the fish species composi-

[9]Stauffer, T. M. 1975. Population characteristics and summer-to-autumn survival of juvenile rainbow trout and coho salmon in two Lake Superior tributaries, 1969-1972. Mich. Dep. Nat. Resour., Fish. Res. Rep. 1825, 21 p. Institute for Fisheries Research, Museums Annex Building, Ann Arbor, MI 48109.

[10]Hannuksela, P. R. 1973. Food interrelationships of the mottled sculpin, *Cottus bairdi*, and juveniles of the rainbow trout, *Salmo gairdneri*, in a tributary of Lake Superior. Mich. Dep. Nat. Resour., Fish. Res. Rep. 1801, 21 p. Institute for Fisheries Research, Museums Annex Building, Ann Arbor, MI 48109.

tion of Lake Ontario. Great Lakes Fish. Comm. Tech. Rep. 23, 65 p.

GOODNIGHT, W. H., AND T. C. BJORNN.
1971. Fish production in two Idaho streams. Trans. Am. Fish. Soc. 100:769-780.

HASSINGER, R. L., J. G. HALE, AND D. E. WOODS.
1974. Steelhead of the Minnesota north shore. Minn. Dep. Nat. Resour., Tech. Bull. 11, 38 p.

HUNT, R. L.
1966. Production and angler harvest of wild brook trout in Lawrence Creek, Wisconsin. Wis. Conserv. Dep. Tech. Bull. 35, 52 p.

JOHNSON, J. H.
1978. Natural reproduction and juvenile ecology of Pacific salmon and steelhead trout in tributaries of the Salmon River, New York. M.S. Thesis, State Univ. New York, Syracuse, 133 p.

O'CONNER, J. F., AND G. POWER.
1976. Production by brook trout (*Salvelinus fontinalis*) in four streams in the Matamek watershed, Quebec. J. Fish. Res. Board Can. 33:6-18.

PARSONS, J. W.
1973. History of salmon in the Great Lakes, 1850-1950. U.S. Bur. Sport Fish. Wildl. Tech. Pap. 68, 80 p.

RICKER, W. E.
1975. Computation and interpretation of biological statistics of fish populations. Fish. Res. Board Can., Bull. 191, 382 p.

SCOTT, W. B., AND E. J. CROSSMAN.
1973. Freshwater fishes of Canada. Fish. Res. Board Can., Bull. 184, 966 p.

SMITH, S. H.
1968. Species succession and fishery exploitation in the Great Lakes. J. Fish. Res. Board Can. 25:667-693.

STEIN, R. A., P. E. REIMERS, AND J. D. HALL.
1972. Social interaction between juvenile coho (*Oncorhynchus kisutch*) and fall chinook salmon (*O. tshawytscha*) in Sixes River, Oregon. J. Fish. Res. Board Can. 29:1737-1748.

WELLS, L., AND A. L. MCLAIN.
1973. Lake Michigan: Man's effects on native fish stocks and other biota. Great Lakes Fish. Comm. Tech. Rep. 20, 55 p.

JAMES H. JOHNSON

New York State Department of Environmental Conservation
50 Wolf Road
Albany, NY 12233

ERRATA

Fishery Bulletin, Vol. 77, No. 4

Caillouet, Charles W., Frank J. Patella, and William B. Jackson, "Trends toward decreasing size of brown shrimp, *Penaeus aztecus*, and white shrimp, *Penaeus setiferus*, in reported annual catches from Texas and Louisiana," p. 985-989.

1) Page 987, left colum, last line, correct line to read:
   $\ln F_i = \ln(a) + bC_i + \epsilon$
2) Page 989, Table 3, first line, under Brown shrimp, Texas coast, 1961-1976, correct line to read:
   0.00141* (adding asterisk)

INFORMATION FOR CONTRIBUTORS TO THE *FISHERY BULLETIN*

Manuscripts submitted to the *Fishery Bulletin* will reach print faster if they conform to the following instructions. These are not absolute requirements, of course, but desiderata.

CONTENT OF MANUSCRIPT

The **title page** should give only the title of the paper, the author's name, his affiliation, and mailing address, including ZIP code.

The **abstract** should not exceed one double-spaced page.

In the **text,** *Fishery Bulletin* style, for the most part, follows that of the *U.S. Government Printing Office Style Manual.* Fish names follow the style of the American Fisheries Society Special Publication No. 6, *A List of Common and Scientific Names of Fishes from the United States and Canada,* Third Edition, 1970.

Text footnotes should be typed separately from the text.

Figures and **tables,** with their legends and headings, should be self-explanatory, not requiring reference to the text. Their placement should be indicated in the right-hand margin of the manuscript.

Preferably **figures** should be reduced by photography to 5¾ inches (for single-column figures, allowing for 50% reduction in printing), or to 12 inches (for double-column figures). The maximum height, for either width, is 14 inches. Photographs should be printed on glossy paper.

Do not send original drawings to the Scientific Editor; if they, rather than the photographic reductions, are needed by the printer, the Scientific Publications Office will request them.

Each **table** should start on a separate page. Consistency in headings and format is desirable. Vertical rules should be avoided, as they make the tables more expensive to print. Footnotes in tables should be numbered sequentially in arabic numerals. To avoid confusion with powers, they should be placed to the *left* of numerals.

Acknowledgments, if included, are placed at the end of the text.

Literature is cited in the text as: Lynn and Reid (1968) or (Lynn and Reid 1968). All papers referred to in the text should be listed alphabetically by the senior author's surname under the heading "Literature Cited." Only the author's surname and initials are required in the **literature cited.** The accuracy of the **literature cited** is the responsibility of the author. Abbreviations of names of periodicals and serials should conform to *Biological Abstracts List of Serials with Title Abbreviations. (Chemical Abstracts* also uses this system, which was developed by the American Standards Association.)

Common **abbreviations** and **symbols,** such as mm, m, g, ml, mg, ° C (for Celsius), %, ‰ and so forth, should be used. Abbreviate units of measure only when used with numerals. Periods are only rarely used with abbreviations.

We prefer that **measurements** be given in metric units; other equivalent units may be given in parentheses.

FORM OF THE MANUSCRIPT

The original of the manuscript should be typed, double-spaced, on white bond paper. Please triple space above headings. We would rather receive good duplicated copies of manuscripts than carbon copies. The sequence of the material should be:

TITLE PAGE
ABSTRACT
TEXT
LITERATURE CITED
APPENDIX
TEXT FOOTNOTES
TABLES (Each table should be numbered with an arabic numeral and heading provided)
LIST OF FIGURES (Entire figure legends)
FIGURES (Each figure should be numbered with an arabic numeral; legends are desired)

ADDITIONAL INFORMATION

Send the ribbon copy and two duplicated or carbon copies of the manuscript to:

Dr. Carl J. Sindermann, Scientific Editor
Fishery Bulletin
Northeast Fisheries Center
Sandy Hook Laboratory
National Marine Fisheries Service, NOAA
Highlands, NJ 07732

Fifty **separates** will be supplied to an author free of charge and 100 supplied to his organization. No covers will be supplied.

O'CONNELL, CHARLES P. Percentage of starving northern anchovy, *Engraulis mordax*, larvae in the sea as estimated by histological methods 475
EBEL, WESLEY J. Transportation of chinook salmon, *Oncorhynchus tshawytscha*, and steelhead, *Salmo gairdneri*, smolts in the Columbia River and effects on adult returns 491
BENIRSCHKE, K., MARY L. JOHNSON, and ROLF J. BENIRSCHKE. Is ovulation in dolphins, *Stenella longirostris* and *Stenella attenuata*, always copulation-induced? 507

Notes

PEARCY, WILLIAM G. A large, opening-closing midwater trawl for sampling oceanic nekton, and comparison of catches with an Isaacs-Kidd midwater trawl .. 529
COE, JAMES M., and WARREN E. STUNTZ. Passive behavior by the spotted dolphin, *Stenella attenuata*, in tuna purse seine nets 535
KRAEUTER, JOHN N., and MICHAEL CASTAGNA. Effects of large predators on the field culture of the hard clam, *Mercenaria mercenaria* 538
PARKER, KEITH. A direct method for estimating northern anchovy, *Engraulis mordax*, spawning biomass 541
PITCHER, KENNETH W. Food of the harbor seal, *Phoca vitulina richardsi*, in the Gulf of Alaska 544
JOHNSON, JAMES H. Production and growth of subyearling coho salmon, *Oncorhynchus kisutch*, chinook salmon, *Oncorhynchus tshawytscha*, and steelhead, *Salmo gairdneri*, in Orwell Brook, tributary of Salmon River, New York 549

☆ GPO 696-404

DEPARTMENT OF COMMERCE
UNITED STATES OF AMERICA

Fishery Bulletin

Marine Biological Laboratory
LIBRARY
FEB 25 1981
Woods Hole, Mass.

Vol. 78, No. 3 July 1980

HANKIN, DAVID G. A multistage recruitment process in laboratory fish populations: implications for models of fish population dynamics 555
CHENG, LANNA, and ERIC SHULENBERGER. Distribution and abundance of *Halobates* species (Insecta: Heteroptera) in the eastern tropical Pacific 579
SHANE, SUSAN H. Occurrence, movements, and distribution of bottlenose dolphin, *Tursiops truncatus*, in southern Texas 593
LAROCHE, JOANNE LYCZKOWSKI, and SALLY L. RICHARDSON. Reproduction of northern anchovy, *Engraulis mordax*, off Oregon and Washington 603
CLARKE, THOMAS A. Diets of fourteen species of vertically migrating mesopelagic fishes in Hawaiian waters 619
RICE, STANLEY D., and JACK E. BAILEY. Survival, size, and emergence of pink salmon, *Oncorhynchus gorbuscha*, alevins after short- and long-term exposures to ammonia 641
BAILEY, JACK E., STANLEY D. RICE, JEROME J. PELLA, and SIDNEY G. TAYLOR. Effects of seeding density of pink salmon, *Oncorhynchus gorbuscha*, eggs on water chemistry, fry characteristics, and fry survival in gravel incubators 649
LENARZ, WILLIAM H., and PETER B. ADAMS. Some statistical considerations of the design of trawl surveys for rockfish (Scorpaenidae) 659
RICE, D. W., JR., F. L. HARRISON, and A. JEARLD, JR. Effects of copper on early life history stages of northern anchovy, *Engraulis mordax* 675
THEILACKER, GAIL H. Changes in body measurements of larval northern anchovy, *Engraulis mordax*, and other fishes due to handling and preservation 685
MORGAN, STEVEN G. Aspects of larval ecology of *Squilla empusa* (Crustacea, Stomatopoda) in Chesapeake Bay 693
POWELL, ALLYN B., and HERBERT R. GORDY. Egg and larval development of the spot, *Leiostomus xanthurus* (Sciaenidae) 701
CRESSEY, ROGER, and HILLARY BOYLE CRESSEY. Bomolochid copepods parasitic on the eyes of Indo-West Pacific clupeid fishes 715
HOWELL, W. HUNTING. Temperature effects on growth and yolk utilization in yellowtail flounder, *Limanda ferruginea*, yolk-sac larvae 731
BISHOP, JAMES M., JAMES G. GOSSELINK, and JAMES H. STONE. Oxygen consumption and hemolymph osmolality of brown shrimp, *Penaeus aztecus* 741
HORN, MICHAEL H. Diel and seasonal variation in abundance and diversity of shallow-water fish populations in Morrow Bay, California 759

(Continued on back cover)

Seattle, Washington

U.S. DEPARTMENT OF COMMERCE
Philip M. Klutznick, *Secretary*

NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION
Richard A. Frank, *Administrator*
Terry L. Leitzell, *Assistant Administrator for Fisheries*

NATIONAL MARINE FISHERIES SERVICE

Fishery Bulletin

The *Fishery Bulletin* carries original research reports and technical notes on investigations in fishery science, engineering, and economics. The Bulletin of the United States Fish Commission was begun in 1881; it became the Bulletin of the Bureau of Fisheries in 1904 and the Fishery Bulletin of the Fish and Wildlife Service in 1941. Separates were issued as documents through volume 46; the last document was No. 1103. Beginning with volume 47 in 1931 and continuing through volume 62 in 1963, each separate appeared as a numbered bulletin. A new system began in 1963 with volume 63 in which papers are bound together in a single issue of the bulletin instead of being issued individually. Beginning with volume 70, number 1, January 1972, the *Fishery Bulletin* became a periodical, issued quarterly. In this form, it is available by subscription from the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402. It is also available free in limited numbers to libraries, research institutions, State and Federal agencies, and in exchange for other scientific publications.

EDITOR

Dr. Jay C. Quast
Scientific Editor, *Fishery Bulletin*
Northwest and Alaska Fisheries Center
Auke Bay Laboratory
National Marine Fisheries Service, NOAA
P.O. Box 155, Auke Bay, AK 99821

Editorial Committee

Dr. Elbert H. Ahlstrom
National Marine Fisheries Service

Dr. Bruce B. Collette
National Marine Fisheries Service

Dr. Edward D. Houde
University of Miami

Dr. Merton C. Ingham
National Marine Fisheries Service

Dr. Reuben Lasker
National Marine Fisheries Service

Dr. Jerome J. Pella
National Marine Fisheries Service

Dr. Sally L. Richardson
Gulf Coast Research Laboratory

Kiyoshi G. Fukano, Managing Editor

The *Fishery Bulletin* (USPS 090-870) is published quarterly by Scientific Publications Office, National Marine Fisheries Service, NOAA, Room 336, 1700 Westlake Avenue North, Seattle, WA 98109. Controlled circulation paid to Finance Department, USPS, Washington, DC 20260.

Although the contents have not been copyrighted and may be reprinted entirely, reference to source is appreciated.

The Secretary of Commerce has determined that the publication of this periodical is necessary in the transaction of the public business required by law of this Department. Use of funds for printing of this periodical has been approved by the Director of the Office of Management and Budget through 31 March 1982.

Fishery Bulletin

CONTENTS

Vol. 78, No. 3 July 1980

HANKIN, DAVID G. A multistage recruitment process in laboratory fish populations: implications for models of fish population dynamics 555
CHENG, LANNA, and ERIC SHULENBERGER. Distribution and abundance of *Halobates* species (Insecta: Heteroptera) in the eastern tropical Pacific 579
SHANE, SUSAN H. Occurrence, movements, and distribution of bottlenose dolphin, *Tursiops truncatus*, in southern Texas 593
LAROCHE, JOANNE LYCZKOWSKI, and SALLY L. RICHARDSON. Reproduction of northern anchovy, *Engraulis mordax*, off Oregon and Washington 603
CLARKE, THOMAS A. Diets of fourteen species of vertically migrating mesopelagic fishes in Hawaiian waters 619
RICE, STANLEY D., and JACK E. BAILEY. Survival, size, and emergence of pink salmon, *Oncorhynchus gorbuscha*, alevins after short- and long-term exposures to ammonia 641
BAILEY, JACK E., STANLEY D. RICE, JEROME J. PELLA, and SIDNEY G. TAYLOR. Effects of seeding density of pink salmon, *Oncorhynchus gorbuscha*, eggs on water chemistry, fry characteristics, and fry survival in gravel incubators 649
LENARZ, WILLIAM H., and PETER B. ADAMS. Some statistical considerations of the design of trawl surveys for rockfish (Scorpaenidae) 659
RICE, D. W., JR., F. L. HARRISON, and A. JEARLD, JR. Effects of copper on early life history stages of northern anchovy, *Engraulis mordax* 675
THEILACKER, GAIL H. Changes in body measurements of larval northern anchovy, *Engraulis mordax*, and other fishes due to handling and preservation 685
MORGAN, STEVEN G. Aspects of larval ecology of *Squilla empusa* (Crustacea, Stomatopoda) in Chesapeake Bay 693
POWELL, ALLYN B., and HERBERT R. GORDY. Egg and larval development of the spot, *Leiostomus xanthurus* (Sciaenidae) 701
CRESSEY, ROGER, and HILLARY BOYLE CRESSEY. Bomolochid copepods parasitic on the eyes of Indo-West Pacific clupeid fishes 715
HOWELL, W. HUNTING. Temperature effects on growth and yolk utilization in yellowtail flounder, *Limanda ferruginea*, yolk-sac larvae 731
BISHOP, JAMES M., JAMES G. GOSSELINK, and JAMES H. STONE. Oxygen consumption and hemolymph osmolality of brown shrimp, *Penaeus aztecus* 741
HORN, MICHAEL H. Diel and seasonal variation in abundance and diversity of shallow-water fish populations in Morrow Bay, California 759

(Continued on next page)

Seattle, Washington

1980

For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402—Subscription price per year: $12.00 domestic and $15.00 foreign. Cost per single issue: $3.00 domestic and $3.75 foreign.

FOGARTY, MICHAEL J., DAVID V. D. BORDEN, and HOWARD J. RUSSELL. Movements of tagged American lobster, *Homarus americanus*, off Rhode Island ... 771
RENSEL, JOHN E., and EARL F. PRENTICE. Factors controlling growth and survival of cultured spot prawn, *Pandalus platyceros*, in Puget Sound, Washington 781

Notes

THEILACKER, GAIL H. Rearing container size affects morphology and nutritional condition of larval jack mackerel, *Trachurus symmetricus* 789
CARNEY, ROBERT S., and ANDREW G. CAREY, JR. Effectiveness of metering wheels for measurement of area sampled by beam trawls 791
PITCHER, KENNETH W. Stomach contents and feces as indicators of harbor seal, *Phoca vitulina*, foods in the Gulf of Alaska 797
CHRISTENSEN, DARRYL J., and WALTER J. CLIFFORD. The 1978 spring recreational catch of Atlantic mackerel, *Scomber scombrus*, off the Middle Atlantic region 799
BEARDSLEY, GRANT L. Size and possible origin of sailfish, *Istiophorus platypterus*, from the eastern Atlantic Ocean 805
RICE, STANLEY D., and JACK E. BAILEY. Ammonia concentrations in pink salmon, *Oncorhynchus gorbuscha*, redds of Sashin Creek, southeastern Alaska ... 809
HUNTER, JOHN R., and CAROL A. KIMBRELL. Egg cannibalism in the northern anchovy, *Engraulis mordax* 811
QUINN, THOMAS P., BRUCE S. MILLER, and R. CRAIG WINGERT. Depth distribution and seasonal and diel movements of ratfish, *Hydrolagus colliei*, in Puget Sound, Washington 816
PEARSON, WALTER H., PETER C. SUGARMAN, DANA L. WOODRUFF, J. W. BLAYLOCK, and BORI L. OLLA. Detection of petroleum hydrocarbons by the Dungeness crab, *Cancer magister* 821

Notices

NOAA Technical Reports NMFS published during the first 6 months of 1980 827

Vol. 78, No. 2 was published on 17 November 1980.

The National Marine Fisheries Service (NMFS) does not approve, recommend or endorse any proprietary product or proprietary material mentioned in this publication. No reference shall be made to NMFS, or to this publication furnished by NMFS, in any advertising or sales promotion which would indicate or imply that NMFS approves, recommends or endorses any proprietary product or proprietary material mentioned herein, or which has as its purpose an intent to cause directly or indirectly the advertised product to be used or purchased because of this NMFS publication.

A MULTISTAGE RECRUITMENT PROCESS IN LABORATORY FISH POPULATIONS: IMPLICATIONS FOR MODELS OF FISH POPULATION DYNAMICS[1]

DAVID G. HANKIN[2]

ABSTRACT

Laboratory studies have been previously used to examine fundamental aspects of fish population dynamics and may be explicitly structured to examine the stock-recruitment relation. Previous studies have shown that cycling of population numbers occurs in refuge-free environments, but provision of refuge areas allows maintenance of stable population numbers. Results of these studies may be adequately explained by simple stock-recruitment theory.

Laboratory experiments described here show that manipulation of refuge habitat quality can profoundly influence interactions among population components. Complex interactions among fry, juveniles, and adults created erratic pulses in numerical population growth. Numerical population dynamics could not be adequately explained by simple stock-recruitment theory.

Based on experimental observations, a multistage adult-juvenile stock-recruitment relation was developed and was found, through statistical analyses, to adequately describe observed numerical dynamics. The biological plausibility of complex multistage recruitment processes argues that expectations for empirical support of simple stock-recruitment theory may be unreasonable and inappropriate. The simple theory may often not be biologically appropriate and more complex models of numerical population dynamics may be required for biological realism and for meaningful data analysis. Whether collection of data necessary to allow use of such complex recruitment models is economically feasible and, if so, whether more complex models may prove of practical use for management of fish populations is at present unclear.

One poorly understood population process is the so-called stock-recruitment relation (Ricker 1954) describing the dependency of input of new individuals, R_t, on the density of adult parents some time previous, $S_{t-\tau}$. Although the theoretical basis of the stock-recruitment relation is well established (Ricker 1954; Beverton and Holt 1957) and recent study in theoretical ecology (May 1975; Oster 1975) has emphasized the impressive variety of population behaviors suggested by simple discrete-time models of the form $R_t = S_{t-\tau} \cdot G(S_{t-\tau})$, remarkably little empirical support for the theory exists. In part this reflects severe restrictions in data collection. In temperate populations, for example, only one observation of recruitment may be obtained annually and this observation is normally related not only to parent stock but also to fluctuating environmental conditions and mortality (from birth to recruitment) which may strongly influence the ultimate size of a recruited year class or cohort. The data collection process is exceedingly slow, and exogenous factors may confound the dependency of recruitment on parent stock.

Further, the theory itself is simplistic. Chief limitations are the requirements that feedback be exerted at only one point in time and that the responsible population component consists solely of adults. Alternative feedback control mechanisms could involve either juveniles or the adult stock at more than one point in time. For example, in largemouth bass, *Micropterus salmoides*, adults are in contact with developing larvae for only a short period of time during which adult-related density-dependent mortality might occur. Adults leave inshore nesting and nursery areas shortly after spawning, but yearling bass, produced by the adult stock a year previous, remain in inshore areas where they may prey extensively on younger juveniles (Ricker 1954). In Dungeness crab, *Cancer magister*, and other cannibalistic species, recruitment may depend not only on parent stock but also on adult densities when juveniles first enter the adult population and are extremely

[1]Based on a dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, Department of Natural Resources, Cornell University.

[2]Department of Natural Resources, Cornell University, Ithaca, N.Y.; present address: Department of Fisheries, Humboldt State University, Arcata, CA 95521.

Manuscript accepted: February 1980.
FISHERY BULLETIN: VOL. 78, NO. 3, 1980.

vulnerable (Butler 1961; Gotshall 1978). The behavior of mathematical models describing such multiple adult feedback mechanisms, termed "multistage" recruitment processes, has been recently investigated by McKelvey et al. (in press). Collection of data suitable for analysis of these more complex models would seem to pose difficulties far in excess of those required for the simple models. In such cases experimental laboratory studies may be more effective and more efficient than "field" investigations for providing insight into the fundamental problem of stock and recruitment.

Laboratory studies of stock and recruitment have many advantages over similar studies of natural wild populations. Strict environmental control (of food supply, temperature, dissolved oxygen, photoperiod, habitat dimension and type), elimination of sampling error through complete enumeration, and opportunity for unique behavioral observations in an aquatic environment are the most obvious. Less obvious but perhaps more significant advantages include the investigator's unrestricted manipulative control over population size and age structure, so that the chief modes of regulation are likely to be endogenous population mechanisms, causally density-dependent, and the opportunity for replication in quantity.

From the perspective of statistical analysis, the influence of exogenous, density-independent factors is reduced, observations may be collected over as wide a range of population states as desired, and (through replication) the inherent variability of the dynamic population processes themselves may be examined (Royama 1977).

Among fishes the study of laboratory populations has centered on a single species, the guppy, *Poecilia reticulata*. The characteristics of small size, rapid maturity, frequent and repeated reproduction, and a relatively short life span render the guppy an ideal subject for laboratory study of the stock-recruitment relation. Basic information has been gathered regarding reproduction (Felin 1935; Purser 1938; Turner 1937; Rosenthal 1952), fecundity (Felin 1935; Hester 1964), and growth (von Bertalanffy 1938), and there have been many, often long-term, studies of population behavior (Breder and Coates 1932; Shoemaker 1944; Silliman 1948, 1968; Silliman and Gutsell 1958; Laakso 1959; Warren 1973; Yamagishi 1976). While the focus of these studies has not been the stock-recruitment relation per se, it is often possible to interpret observed population dynamics in part as a reflection of an overcompensatory function relating numerical population addition to densities of adult fish.

The guppy is a viviparous member of the family Poeciliidae and exhibits strong sexual dimorphism. The maximum weight for mature males is perhaps 0.2-0.4 g as compared with a maximum weight for females of perhaps 1-2 g. Sexual maturity is normally reached by both males and females at 12-16 wk at weights of 0.1-0.15 and 0.2-0.3 g. Average longevity under laboratory conditions might be 12-18 mo. Young are produced in discrete broods, ranging in size from 2 or 3 to 50, at roughly monthly intervals at 25° C. Brood size depends on female size and, as a result, the appropriate measure of adult reproductive potential is not the number of adults but, since fecundity is nearly proportional to female weight, the total adult female biomass. Males mate freely and indiscriminantly with available females, and sperm from a single mating may remain viable and produce successive broods for periods up to 6 mo (Winge 1937). Females are clearly the overwhelmingly important component of the adult stock.

At birth fry weigh 7-8 mg and, immediately after ejection by females, are extremely vulnerable to predation by adults. Cannibalism has been regarded as the primary feedback mechanism controlling population size (Breder and Coates 1932; Laakso 1959). Recent experiments have suggested that cannibalism is chiefly a function of contacts between individuals rather than of responses to limitations in food supply (Silliman 1968; Warren 1973).

Laboratory environments for guppy population study have differed significantly in two respects: food supply and provision of refuge areas. Food has been delivered at either fixed and limiting or "to excess" ration levels, and refuge areas have only rarely been provided. These studies have shown that total population biomass is strongly influenced by food supply (Silliman 1968), but numerical densities and dynamics are strongly affected by refuge area provision and only slightly influenced by food supply.

Cycles of abundance have been observed in all long-term studies where refuge areas have been absent (Breder and Coates 1932; Shoemaker 1944; Laakso 1959). Characteristics of abundance cycles (begun with small numbers of adults) include initial increases in numbers, reduction of such increases to near zero as adult predator density

becomes large, shift to an adult-dominated age structure, and reappearance of young individuals when adult density declines through mortality to levels at which fry survival once more occurs. In those few instances in which refuge habitats have been provided (Silliman 1948, 1968; Silliman and Gutsell 1958), the results have demonstrated that roughly stable populations, of greater numerical size, with finely graded age (or size) structure, may be maintained for apparently indefinite periods. Presumably, the stability of these populations reflects the decreased period of time during which fry are vulnerable to cannibalism.

In previous guppy population studies the weight of the mature female stock has not been recorded and hence it is impossible to attempt an adequate quantitative examination of stock-recruitment relations which may have been responsible for observed dynamics (e.g., Gulland 1962 based on previous studies). The experiments described on the following pages were specifically designed to allow quantitative assessment of the stock-recruitment relation. Refuge areas were provided and fry successfully entering these areas were considered as rough equals of recruited fish. Although females do not release broods synchronously (broods are delivered continuously with respect to the entire population), data were collected at discrete biweekly intervals. Net numerical change in a sampling interval could thus be related to adult reproductive potential and adult predator density at the beginning of an interval in a fashion analogous to that which might be attempted in analysis of the simple discrete-time models. A simple difference in refuge design (as compared with Silliman's earlier work) involving spacing between glass rods in a refuge fence, however, created unexpected patterns of numerical increase. These patterns were not anticipated and could not be explained on the basis of simple stock-recruitment theory. Analysis ultimately showed the presence of a complex mechanism involving both adult and immature population components, an adult-juvenile stock-recruitment relation.

METHODS AND MATERIALS

Experiments were performed in a 3 m × 3.7 m room insulated on three walls, including two outside walls, from floor to ceiling. A small electric floor heater maintained room temperature at approximately 22° C, about 3° C above ambient winter temperature supplied by a propane heating unit in an adjoining room. An air-conditioner in the same adjoining room prevented summer temperatures from exceeding 26° C. Experimental aquaria were located along the three insulated walls.

Experimental Environments

Twelve aquaria, of dimensions 31 cm × 62 cm × 41 cm, each holding about 80 l of water, served as experimental units. Each aquarium was equipped with a 75 W thermostat-controlled aquarium heater, about 1 cm deep layer of 3-5 mm gravel, a large inside-type charcoal-glass wool filter, a full hood reflector with two 15 W showcase bulbs, a thermometer, and a refuge area (Figure 1). Refuge areas were enclosed by a fence consisting of two sheets of solid glass rods, 3 mm in diameter, spaced (initially) 5 mm apart on centers, fitted in Plexiglas[3] frames glued at right angles. The

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

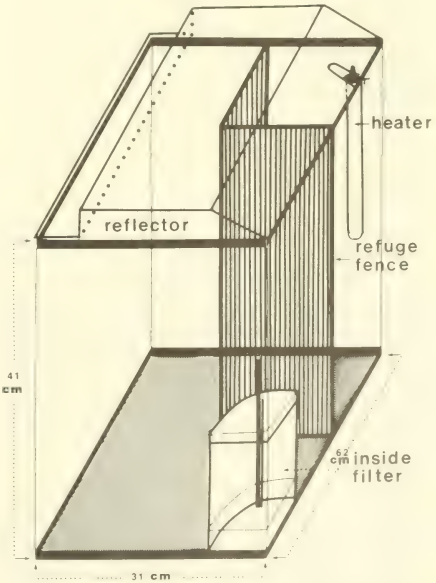


FIGURE 1.—Schematic of the experimental environments for guppies and southern platyfish.

fences partitioned off corners of aquaria, roughly 15 cm × 15 cm of aquaria bottoms, extended from aquaria bottoms to aquaria frames above the water level, and reserved about one-eighth of the total volume as refuge and nursery areas for fry. A 2 cm high Plexiglas frame surrounded both sides of a refuge fence base, preventing gravel from interfering with fence manipulation and allowing easy removal and replacement of the fence at population enumerations.

Light was provided for 12 h per day and was regulated by electric timers. To ensure standardized lighting conditions in all aquaria, the two 62 cm sides of an aquarium were covered with opaque polyethylene sheeting; of the two remaining sides, one abutted the wall and the other was left clear for observations of population behavior. Temperatures were maintained at approximately 25.5° C with a maximum recorded range in all aquaria over a 58-wk period of roughly 24°-28° C. Temperatures were monitored and recorded every 2 d. Air for filter units was supplied by small air pumps.

At weekly intervals filter units were cleaned, charcoal and glass wool replaced, and about 16 l of aquarium water and detritus were siphoned from each aquarium bottom and replaced with aged aerated water. A diatomaceous earth power filter was used weekly for 60-90 min periods per aquarium and helped maintain water quality.

Routine Experimental Manipulations

Feeding

Populations were fed accurately weighed amounts of food twice daily. Morning feedings consisted of dried food only (Tetramin brand Conditioning Food). Evening feedings consisted of thawed, rinsed, and drained adult brine shrimp, *Artemia salina*, and newly hatched *Artemia* nauplii. Nauplii were suspended in freshwater and pipetted directly into the refuge areas while dried food and adult brine shrimp were delivered to the main aquarium volume outside the refuge area.

Since no technical assistance was available to daily siphon uneaten food from aquaria, it was not possible to maintain a steady fixed ration level throughout the experimental period. Instead, rations of dried food and of adult brine shrimp were increased in increment steps as populations grew, maintaining a relatively constant ratio of food supply to population biomass during initial stages of population growth. Food supply became fixed when populations had achieved about 50% of the apparent maximum biomass supported at the final fixed ration level. The increment steps prevented deterioration of water quality through decomposition of uneaten food and allowed for subsequent analysis of changes in population biomass as related to food supply. Exact ration levels and corresponding dates appear in the section on experimental design.

Marking

At triweekly intervals a fluorochrome, DCAF (2,4 bis (N,N′ di/carboxymethyl/aminomethyl) fluorescein), was incorporated into the adult brine shrimp ration component. The DCAF-laden shrimp was fed twice daily for 3-d periods at ration levels corresponding to the normal adult brine shrimp feeding for the period. Dried food was not fed during marking intervals. Marking trials had indicated that circular fluorescent rings corresponding to time of injestion of DCAF were produced on the growing margin of guppy scales. Repeated marks could be produced by repeated administration at intervals exceeding 1 wk. Marking was designed to allow assessment of age structure at conclusion of the experiments from analysis of fluorescent marks on scales removed from fish. Scales were removed from samples of fish from all populations at week 36 and at week 58. Details of marking procedures may be found in Hankin (1978a).

Data Collection

At biweekly intervals complete enumeration of populations was performed. In early weeks (0-14) enumeration was staggered by 1 wk so that four populations and eight populations were enumerated on alternate weekends. In later weeks (14-58) all populations were enumerated in a 2-d interval at biweekly intervals.

All fish were removed from individual aquaria during enumerations and separated by size categories. Glass rod-Plexiglas grading devices, similar in design to refuge fences, were used to separate fish on the basis of "diameter" (or more correctly, maximum breadth). During weeks 0-36 six size categories were monitored, and two additional categories were included during weeks 36-58. A description of the size structure classifi-

cation achieved by the grading process and size category designations are contained in Table 1. These size category designations will be adopted throughout the paper for brevity.

After separation into size categories, numbers of males and females in each size category were recorded, and weights of males and females in size categories A_6, A_7, A_8 (weeks 0-36) and $A_{5.5}$, A_6, A_7, A_8 (weeks 36-58) were obtained separately. Weights of fry were not obtained due to dangers of handling mortality. Weights of remaining size categories were obtained without separation by sex as these groups contained nearly all immature fish. To determine weights, fish were placed in a small nylon net, blotted on paper towels until no further moisture was observed (about 1 min), and then transferred to a previously weighed plastic beaker containing about 40 ml of water. Weights of fish were determined as the difference between the previous weight and the weight obtained after addition of fish. Total population biomass was determined as the sum of all weight measurements for a given population but did not include weight of fry. An Ainsworth Model 10N analytical balance, accurate to three decimal places, was used for all weighings. Handling mortality was negligible. In 58 wk only five mortalities, all fish <2 mm in "diameter," were recorded as a direct result of biweekly manipulations at enumeration. Approximately 38,000 fish were handled during these enumerations.

All fish were also examined for external symptoms of disease at biweekly enumerations. Disease diagnosis and/or confirmation was performed at irregular intervals by Louis Leibovitz, Cornell University Veterinary School. Fish with obvious external disease symptoms (consistently diagnosed as chronic piscine tuberculosis) but otherwise apparently healthy were treated by a 20-min bath in Formalin (1:4,000). Severely afflicted fish near death were removed from populations and counted as mortalities. Numbers, weights, and sexes of fish showing symptoms and/or treated were recorded for each population at enumeration. Aquaria were examined daily for mortalities. Date of death, size category estimate, and sex were recorded for each observed mortality.

At termination (week 58) a sample of 41 gravid females ranging from 21 to 39 mm was selected from the populations. Each female was dissected and the number of embryos counted. Data collected was used to establish an overall relation between fecundity and female size for the experimental populations.

TABLE 1.—Size-group classifications of guppies at enumerations during weeks 0-36 (Phase I) and weeks 36-58 (Phase II). Grader spacing is measured from center to center.

Weeks	Size-group designation	Grader spacing (mm)	Fish diameter range (mm)	Description
0-36	Fry	4	<1	Newly born fry
	J_4	4	1-2	All immature
	J_5	5	2-3	Immature males and females, mature males
	A_6	6	3-4	Largest mature males, small mature females
	A_7	7	4-5	Large mature females
	A_8	8	>5	Largest mature females
36-58	Fry	4	<1	Newly born fry
	$J_{4.0}$	4	1-1.5	All immature
	$J_{4.5}$	4.5	1.5-2	All immature
	$J_{5.0}$	5.0	2-2.5	Immature females, maturing males
	$A_{5.5}$	5.5	2.5-3	Maturing females, mature males
	A_6	6	3-4	Largest mature males, small mature females
	A_7	7	4-5	Large mature females
	A_8	8	>5	Largest mature females

Experimental Design

The initial intent of population experiments was to examine dynamics of mixed species populations (guppies, *P. reticulata*, and southern platyfish, "platy," *Xiphophorous maculatus*) from the perspective of stock-recruitment theory. Due to excessive mortality among the southern platyfish and an apparent inability of their fry to successfully compete with guppy fry, the southern platyfish were removed from all populations at week 8 and experimental goals became limited to analysis of single species populations based on simple stock-recruitment theory. Numerical population growth of single species populations, however, was not anticipated on the basis of the simple theory. Numerical population growth often occurred as a series of discrete pulses of increase, followed by periods of roughly static population numbers. Behavioral observations and analyses of collected population data through week 36 indicated that the pulsing quality of numerical growth was probably caused by juvenile-fry interactions within refuge areas. Based on this hypothesis, experimental populations were manipulated and exposed to different treatments at week 36. Treatment consisted of alteration of original refuge area habitat quality and population growth under these new conditions was monitored through week 58 to test the juvenile-fry interaction hypothesis.

The experiments have been separated into two distinct phases based on the above-described ex-

perimental path. Weeks 0-36, which included original mixed species populations and subsequent unexpected behavior of single species populations, may be regarded as exploratory in nature and have been designated Phase I. The test of the juvenile-fry interaction hypothesis, during weeks 36-58, may be considered confirmatory in nature and has been designated Phase II. The logic of the experimental path is depicted in Figure 2. Experimental observations collected during Phase I were indeed responsible for the development of the juvenile-fry hypothesis tested during Phase II.

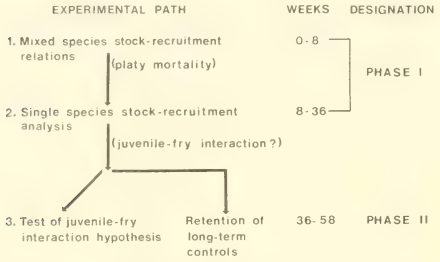


FIGURE 2.—The experimental design for guppy and southern platyfish (platy) populations.

Phase I (Weeks 0-36)

WEEKS 0-8.—Twelve experimental aquaria were grouped into three blocks of four aquaria each and each block was assumed to have equal position effect (Figure 3). Blocks A and C contained replicate groups of four mixed species populations each. Block B had replicate single species guppy populations (aquaria 5 and 6) and platy populations (aquaria 7 and 8). A gold strain of guppies was used to allow visual separation of

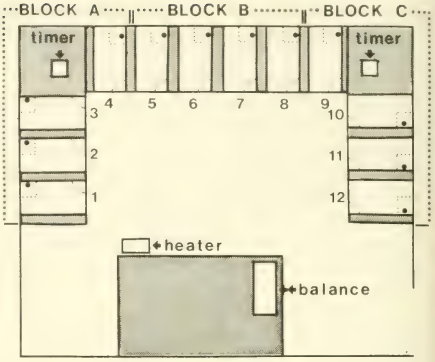


FIGURE 3.—Schematic of the laboratory facility showing blocking of experimental aquaria for guppy and southern platyfish populations.

guppy and platy fry at birth, otherwise difficult with wild-type strains. Weights, sex, and numbers of each species initially stocked in aquaria are listed in Table 2. Estimated age of both guppies and platies at stocking was 14-18 wk.

All populations were fed rations containing approximately equal proportions of the food items with the exception of *Artemia* nauplii. All populations received a fixed daily ration of *Artemia* nauplii, 0.2 g. Total rations were increased in stepwise increments to keep the daily wet weight equivalent of rations at from 25 to 35% of total population biomass. Since growth of guppies appeared more rapid in mixed species populations, single species population rations were increased in rapid increments at the end of week 6. Food rations supplied to populations during the first 8 wk are in Table 3. At the end of week 8 all platies were removed from mixed species populations and

TABLE 2.—Stocking of guppies and southern platyfish at initiation of experiments, 5 June 1975. Weights (grams) in parentheses.

Block	Tank number	Guppies			Southern platyfish			Tank totals
		Female	Male	Total	Female	Male	Total	
A	1	5(2.540)	4(0.581)	9(3.121)	4(3.488)	4(2.188)	8(5.676)	17(8.797)
A	2	5(2.452)	4(0.599)	9(3.051)	4(3.668)	4(2.359)	8(6.027)	17(9.078)
A	3	5(2.548)	4(0.590)	9(3.138)	4(3.788)	4(1.861)	8(5.649)	17(8.787)
A	4	5(2.574)	4(0.664)	9(3.238)	4(3.455)	4(2.155)	8(5.610)	17(8.848)
B	5	5(2.639)	4(0.655)	9(3.294)				9(3.294)
B	6	5(2.746)	4(0.677)	9(3.423)				9(3.423)
B	7				4(4.038)	4(2.568)	8(6.606)	8(6.606)
B	8				4(4.176)	4(2.511)	8(6.687)	8(6.687)
C	9	5(2.521)	4(0.654)	9(3.175)	4(3.550)	4(2.152)	8(5.702)	17(8.877)
C	10	5(2.355)	4(0.542)	9(2.897)	4(3.553)	4(2.198)	8(5.751)	17(8.648)
C	11	5(2.288)	4(0.605)	9(2.893)	4(3.470)	4(2.161)	8(5.631)	17(8.524)
C	12	5(2.290)	4(0.675)	9(2.965)	4(3.762)	4(2.230)	8(5.992)	17(8.957)

TABLE 3.—Schedule of daily rations fed to guppy and southern platyfish populations during weeks 0-8. Total is expressed as a wet weight equivalent.[1]

Dates (1975)	Weeks	Dry food (g)	*Artemia* adults (g)	*Artemia* nauplii (g)	Total (g)
Mixed-species populations (populations 1-4, 9-12)					
2 June- 6 July	0-4	0.2	1.0	0.2	3.2
7 July - 3 Aug.	4-8	0.15	1.25	0.2	2.95
Single species populations					
Guppies (populations 5, 6)					
2 June-21 June	0-2	0.08	0.4	0.08	1.28
22 June- 6 July	2-4	0.08	0.4	0.2	1.4
7 July -20 July	4-6	0.06	0.6	0.2	1.4
21 July -22 July	—	0.08	0.8	0.2	1.8
23 July - 3 Aug.	6-8	0.10	1.0	0.2	2.2
Southern platyfish (populations 7, 8)					
2 June-21 June	0-2	0.15	0.75	0.15	2.4
22 June- 6 July	2-4	0.15	0.75	0.2	2.45
7 July - 3 Aug.	4-8	0.10	1.0	0.2	2.2

[1]To determine, multiply dry food ration by 10 and add all food types.

rations were reduced to equal ration levels in original single species guppy populations.

WEEKS 8-36.—Neither guppy population biomass nor numbers at week 8 differed significantly between original single species populations and mixed species populations so the 10 remaining populations were considered replicates during weeks 8-36. To eventually achieve population age structure which would be finely graded and to achieve equality in numbers of original females in all aquaria, the original females were gradually "phased out" by removal of one adult female from each population at weeks 11, 13, 15, and 17. Original females were easily separated from recently matured female progeny by their larger size and were removed by selecting the smallest female first, in each population, to least affect population biomass. Food rations were increased in stepwise increments through week 22 after which time rations were fixed. A slight departure occurred during weeks 28-29 when dried food only was fed twice daily (Table 4).

TABLE 4.—Schedule of daily rations fed to guppy populations during weeks 8-36. Total is expressed as a wet weight equivalent.[1]

Dates (1975-76)	Weeks	Dry food (g)	*Artemia* adults (g)	*Artemia* nauplii (g)	Total (g)
3 Aug. -19 Aug.	8-10	0.10	1.0	0.20	2.2
20 Aug. -17 Sept.	10-14	0.13	1.3	0.20	2.8
17 Sept.-28 Oct.	14-20	0.15	1.5	0.20	3.2
29 Oct. -12 Nov	20-22	0.18	1.8	0.20	3.8
13 Nov. -21 Dec.	22-28	0.20	2.0	0.20	4.2
22 Dec. -30 Dec.	28-29	[2]0.40	—	—	4.0
31 Dec. -15 Feb.	29-36	0.20	2.0	0.20	4.2

[1]To determine, multiply dry food by 10 and add all ration types.
[2]0.20 g fed twice daily. Three morning feedings were missed during this period.

Phase II (Weeks 36-58)

Three populations (5, 6, and 12) from the original 10 were selected at random to be long-term controls. Of the remaining seven populations, two pairs (1 and 2, 4 and 10) were mixed and divided to give three approximately comparable populations (for each mixed pair) of reduced numerical size and biomass. The remaining three populations were simply reduced in size to similar levels. Numbers of individuals in reduced populations ranged from 74 to 81, of which 42-49 were adults in size categories $\geq A_{5.5}$ (the largest adult male and smallest adult female size category, see Table 1). Total reduced population biomass ranged from 12 to 14 g, slightly less than one-half of apparent maximum population biomass.

The nine reduced populations produced in the above manner were assigned to three groups of three each for treatment. Treatment consisted of replacing original 5.0 mm spacing (on centers) refuge fences with refuge fences of 4.5, 5.0, or 5.5 mm spacing. Each group contained two populations of mixed population origin and one which had been reduced from a larger single population. Refuge areas were assigned to populations with the restriction that each of the three populations produced from a mixed pair must be assigned a different refuge fence spacing. A summary of manipulations at week 36 is presented in Table 5. Daily rations for Phase II are presented in Table 6.

RESULTS

Phase I

Weeks 0-8

The attempt to examine stock-recruitment relations in mixed species populations failed due to high platy mortality in certain aquaria and an apparent inability of platy fry to successfully compete with guppy fry for food. Relative competitive ability of platy and guppy fry was reflected in contrasting mean weights of platy juveniles in mixed and single species populations at the end of week 8. Mean weights of platy juveniles, all born during the first 2 wk of the experiments, were 0.0144 g in a mixed species population and 0.1037 g in a single species population at week 8. Guppy juveniles, also presumably born within the first 2 wk, had reached a mean weight of 0.0979 g by week 8 in the same mixed species population.

TABLE 5.—Manipulations of guppy populations at the end of Phase I (week 36) for test of refuge fence spacing treatment effect during Phase II (weeks 36-58).

Tank number	Refuge assignment (mm)	Origin
1	5.0	No. 1 and 2, mixed and reduced[1]
2	5.5	No. 1 and 2, mixed and reduced[1]
3	5.0	No. 3, reduced
4	4.5	No. 4 and 10, mixed and reduced[2]
5	5.0	"Long-term control"
6	5.0	"Long-term control"
7	4.5	No. 1 and 2, mixed and reduced[1]
8	5.5	No. 4 and 10, mixed and reduced[2]
9	4.5	No. 9, reduced
10	5.0	No. 4 and 10, mixed and reduced[1]
11	5.5	No. 11, reduced
12	5.0	"Long-term control"

[1]Plus eight fry from tank no. 3.
[2]Plus five fry and four $A_{5.5}$ (an adult male size category, refer to Table 1) males from tank no. 11.

TABLE 6.—Schedule of daily rations fed to treated guppy populations during Phase II (weeks 36-58). Total is expressed as a wet weight equivalent.[1]

Dates (1976)	Weeks	Dry food (g)	*Artemia* adults (g)	*Artemia* nauplii (g)	Total (g)
17 Feb.-28 Feb.	36-38	0.15	1.5	0.20	3.2
1 Mar.-15 Mar.	38-40	0.18	1.8	0.20	3.8
16 Mar.-18 Apr.	40-58	0.20	2.0	0.20	4.2

[1]To determine, multiply dry food by 10 and add all ration types.

Since both mixed and single species populations were fed at equal ration levels relative to total population biomass, it seems reasonable to infer a strong competitive advantage to guppy fry in securing food.

In contrast, the presence of platies apparently had little effect on guppy populations in mixed populations. Tests (Student's t) for differences in mean guppy population numbers and biomass between single species and mixed species populations at week 8 failed to reject, at the $\alpha = 0.05$ level, null hypotheses of equality in population numbers or biomass. After removal of platies, all guppy populations were treated as (equivalent) replicates.

Weeks 8-36

The 10 replicate guppy populations through week 36 showed a striking contrast between growth in numbers and growth in biomass. Biomass steadily increased in all populations and weights attained at each sampling period were nearly equal in all populations. Populations seemed near a common maximum supportable biomass by week 36. In contrast, numerical growth was highly variable and often occurred as discrete pulses of increase. Total population numbers always varied greatly among populations and there was no indication of a common approach to an asymptotic or stable numerical population size (Table 7).

BIOMASS DYNAMICS.—In general, biomass growth in all guppy populations was typified by steady, nearly uniform, biweekly increments through the first 28 wk and by declining increments during weeks 28-36. Removals of individual females at weeks 11, 13, 15, and 17 and restriction of rations to dried food only during weeks 28-29 were clearly reflected in depressed biomass increments during these intervals of disturbance (Figure 4). At week 36 mean population biomass was 28.906 g and ranged from 26.291 to 30.717 g.

Using data for weeks 18-28 and 30-36 (periods during which neither removals nor atypical feedings occurred, and beyond the time when platies were also present in certain populations), maximum supportable biomass for each population was estimated by assuming a logistic biomass growth model. Application of the logistic model presumed that biomass growth was limited by the final fixed ration level reached at week 22. Maximum bio-

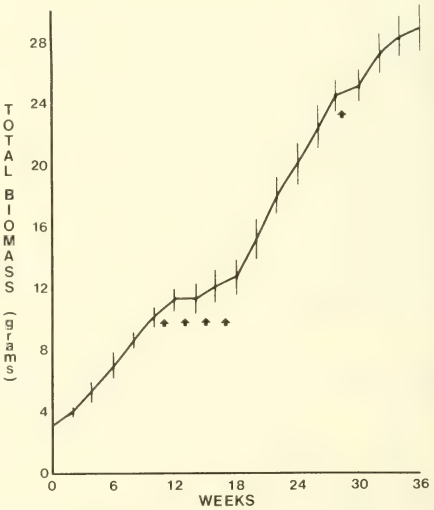


FIGURE 4.—Mean population biomass of guppies during Phase I. Removals of individual females at weeks 11, 13, 15, and 17 and restriction of ration to dried food only during weeks 28-29 are indicated by arrows. Vertical lines represent standard deviations.

TABLE 7.—Total population numbers and, in parentheses, total biomass in grams for single species (guppy) populations at week of enumeration during Phase I, weeks 0-36.

Week	Population number										Mean numbers (SD)	Mean biomass (SD)
	1	2	3	4	5	6	9	10	11	12		
0	9	9	9	9	9	9	9	9	9	9	9	3.120
	(3.121)	(3.051)	(3.145)	(3.238)	(3.294)	(3.423)	(3.175)	(2.897)	(2.893)	(2.965)	(0)	(0.173)
1					9	34					21.5	3.752
					(3.955)	(3.548)					(17.7)	(0.288)
2	29	43	37	31			38	39	40	12	33.6	3.930
	(3.903)	(4.025)	(4.176)	(4.599)			(4.074)	(4.162)	(3.009)	(3.495)	(9.9)	(0.483)
3					38	33					35.5	4.803
					(4.685)	(4.921)					(3.5)	(0.167)
4	53	57	39	50			35	64	32	28	44.8	5.436
	(5.798)	(5.985)	(4.935)	(6.059)			(5.332)	(5.995)	(4.642)	(4.740)	(13.0)	(0.599)
5					43	63					53.0	5.573
					(5.713)	(5.443)					(14.1)	(0.191)
6	72	75	39	58			48	61	33	34	52.5	6.860
	(7.379)	(7.968)	(5.466)	(8.027)			(6.871)	(7.552)	(5.835)	(5.778)	(16.5)	(1.035)
7					41	61					51.0	7.037
					(6.682)	(7.392)					(14.1)	(0.502)
8	91	97	38	69			47	59	33	54	61.0	8.558
	(9.355)	(8.372)	(8.216)	(9.073)			(8.373)	(9.458)	(7.711)	(7.902)	(23.3)	(0.659)
9					39	61					50.0	8.538
					(8.582)	(8.494)					(15.6)	(0.062)
10	108	93	39	83			48	60	32	78	67.6	10.173
	(10.853)	(9.985)	(9.423)	(10.785)			(10.228)	(11.335)	(9.519)	(9.273)	(27.1)	(0.756)
11					40	63					51.5	10.440
					(10.241)	(10.638)					(16.3)	(0.281)
12	136	103	38	89			46	58	62	76	76.0	11.205
	(12.087)	(12.058)	(10.235)	(11.686)			(10.734)	(11.483)	(10.420)	(10.929)	(32.4)	(0.724)
13					38	59					48.5	10.506
					(10.047)	(10.964)					(14.8)	(0.648)
14	158	100	61	88	36	58	46	66	85	100	79.8	11.416
	(12.881)	(12.391)	(10.233)	(12.440)	(10.002)	(10.808)	(11.403)	(12.509)	(10.482)	(11.009)	(35.1)	(1.062)
16	181	106	77	85	36	66	43	74	89	105	86.2	12.137
	(13.762)	(13.253)	(10.794)	(12.989)	(9.934)	(12.419)	(11.908)	(12.552)	(11.447)	(12.309)	(40.5)	(1.158)
18	190	113	92	83	40	92	51	67	84	104	91.6	12.623
	(13.729)	(14.552)	(11.042)	(13.697)	(10.488)	(12.365)	(12.302)	(13.176)	(12.113)	(12.768)	(41.3)	(1.243)
20	190	112	98	81	64	111	82	78	86	103	100.5	15.230
	(16.169)	(17.282)	(13.555)	(15.687)	(12.710)	(15.075)	(14.826)	(15.518)	(15.801)	(15.681)	(35.0)	(1.302)
22	192	112	100	78	73	107	95	92	87	101	103.7	18.097
	(19.709)	(19.688)	(16.151)	(18.502)	(15.989)	(18.555)	(17.354)	(18.571)	(17.545)	(18.906)	(33.3)	(1.311)
24	189	113	98	95	76	104	98	97	85	103	105.8	20.187
	(21.837)	(21.562)	(19.618)	(20.220)	(18.037)	(19.898)	(18.828)	(19.827)	(20.674)	(21.365)	(31.0)	(1.213)
26	191	112	99	127	75	102	96	125	85	102	111.4	22.528
	(24.391)	(24.144)	(21.276)	(22.687)	(20.760)	(23.289)	(21.388)	(21.479)	(22.149)	(23.714)	(32.2)	(1.305)
28	200	111	95	149	75	102	103	130	85	104	115.4	24.519
	(25.953)	(25.886)	(22.705)	(24.824)	(23.305)	(25.171)	(23.810)	(23.890)	(24.361)	(25.284)	(36.4)	(1.091)
30	197	112	107	142	83	102	101	139	138	132	125.3	25.133
	(26.558)	(26.465)	(23.624)	(25.584)	(23.857)	(26.295)	(24.607)	(23.947)	(24.526)	(25.865)	(32.1)	(1.148)
32	194	110	128	151	91	168	101	135	152	160	139.0	27.350
	(28.909)	(28.641)	(26.355)	(27.953)	(26.093)	(27.654)	(26.418)	(25.377)	(27.452)	(28.679)	(32.2)	(1.232)
34	191	118	162	143	98	171	98	149	178	173	148.1	28.395
	(29.614)	(29.580)	(28.085)	(29.099)	(27.548)	(29.842)	(27.327)	(27.104)	(26.150)	(29.599)	(33.4)	(1.316)
36	186	114	178	156	112	197	119	144	186	169	156.1	28.906
	(29.580)	(30.158)	(28.363)	(30.004)	(28.258)	(30.717)	(27.470)	(27.560)	(26.291)	(30.656)	(32.2)	(1.527)

mass for each population was estimated from the slope and intercept of a regression of the reciprocal of population biomass at week $t + 2$ against the reciprocal of biomass at week t as: maximum biomass = $\hat{B}_{max}$ = (1 − slope)/intercept. Estimates of maximum biomass ranged from 27.8 to 37.6 g (Table 8) with a mean estimate of 31.8 g.

The nearly uniform changes in total biomass throughout Phase I, despite widely divergent numerical growth patterns, implied that growth was strongly density-dependent. Density-dependence of growth was seen most dramatically in the mean weights of large adult females. Mean weights of adult females in size categories A_7 and A_8 were inversely related to mean population numbers during weeks 0-36 (Figure 5).

NUMERICAL DYNAMICS.—While the guppy populations appeared to approach a common maximum supportable biomass, no such commonality was evident in total population numbers. Numerically, populations grew in erratic and independent fashion with no clear indications of asymptotic behavior. Numerical growth was steadily positive in only a single population (population 1). In all other populations patterns of numerical increase were unanticipated and often consisted of discrete pulses of increase, followed by periods of static

TABLE 8.—Logistic growth method estimates of maximum biomass (B_{max} in grams) for Phase I guppy populations. Estimates exclude weight of fry and are based on data collected for weeks 18-28, and 30-36.

Population number	r[1]	B_{max}	Population number	r[1]	B_{max}
1	0.992	32.7	6	0.980	32.4
2	.997	33.4	9	.994	30.9
3	.993	32.0	10	.991	29.9
4	.995	37.6	11	.972	27.8
5	.993	30.6	12	.987	31.1

[1]Correlation coefficient for regression of $1/\text{biomass}_{t+2}$ against $1/\text{biomass}_t$.

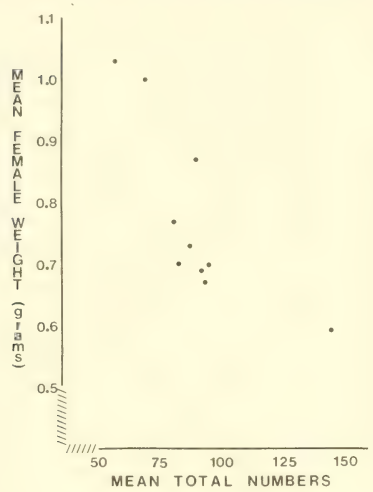


FIGURE 5.—Density-dependence of guppy growth illustrated by plot of mean female weight (in size categories $A_7 + A_8$) at week 36 against mean total numbers during weeks 0-36.

FIGURE 6.—Pulsing behavior of numerical population growth illustrated by guppy populations 3 (solid line) and 11 (dots).

population numbers, followed by further pulses of increase (Figure 6). No position effect was detected when mean total numbers in blocks A and C were compared by Student's t test.

The patterns of numerical increase exhibited by these populations were in striking contrast with the control (unexploited) populations maintained by Silliman and Gutsell (1958). Behavioral observations and examination of size structure data collected during Phase I indicated that the presence of juveniles in the J_4 size category somehow inhibited survival of newly born fry, presumably through some juvenile-fry interaction within the refuge area. Plots of estimated numbers of fry surviving to enumeration during a biweekly interval, corrected for observed mortalities (= adjusted population increment), and numbers of J_4 juveniles present at the beginning of the interval, against time showed distinct offset peaks of abundance in many populations. The relations could be further improved by introducing a 2-wk time lag and plotting the number of J_4 juveniles at $t - 2$ wk and the adjusted population increment from t to $t + 2$ wk against time (Figure 7). The time lag improvement implied that only larger juveniles within the J_4 size category were responsible for inhibition of fry survival. Small J_4 juveniles at $t - 2$ wk would have become large J_4 juveniles (roughly equal to the $J_{4.5}$ size category monitored during Phase II) at time t.

Strong and statistically significant ($P < 0.05$) negative correlations between biweekly adjusted population increments and the natural logarithm of J_4 juveniles (+1) present 2 wk before the beginning of a sampling interval were found in 8 of 10 populations (Table 9). These negative correlations between numerical population growth and juvenile densities detected at several levels of adult stock density showed that numerical population growth, and thus the recruitment process, in these populations could not be a simple function of adult stock alone. Likely, interactions between newly

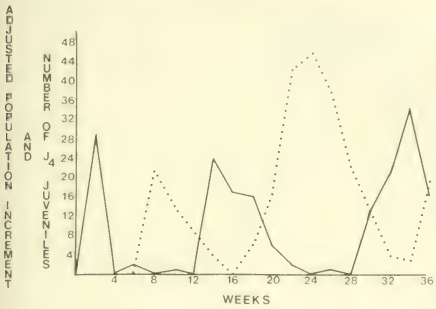


FIGURE 7.—Adjusted population increment (in t, $t + 2$) and number of J_4 guppy juveniles (at $t - 2$) plotted against week (at $t + 2$) in population 3. The plot incorporates a 2-wk time lag. Solid line is adjusted population increment. Dots show juvenile densities.

born fry and immature juveniles had created a complicated population growth process involving both immature and adult population components as had been briefly mentioned by Ricker (1954).

A tentative conceptual model of numerical population dynamics was proposed and is depicted in Figure 8. Survival of newly born fry in a given experimental interval can be viewed as a two-step process. Fry born must first elude adult predators outside the refuge area. Fry which successfully elude adults and enter the refuge area are faced by predation, competition, or harrassment by large J_4 juveniles present in the refuge area. Pulses of numerical increase can easily be created if such a process occurs. Following the initial entrance of fry into the refuge area, growth of fry occurs. Once fry grow to the juvenile size at which interaction with newly born fry occurs, fry survival is inhibited so long as juveniles are smaller than the J_5 size category. Once reaching the J_5 size category, juveniles are transferred to the main aquarium environment at enumeration. The refuge area is once more free of juveniles, and fry successfully eluding adult predators and entering the refuge area are once more expected to survive.

Since the above explanation for the pulsing quality of numerical growth seen in many populations seemed a plausible hypothesis, alteration of the refuge fence design (by either increasing or decreasing spacing between glass rods) would likely increase or decrease the intensity and duration of juvenile-fry interactions within refuge areas. This hypothesis was examined in Phase II.

TABLE 9.—Linear correlation coefficients (r) between adjusted population increment ($API_{t,\,t+2}$) and natural logarithm of juvenile numbers [$\ln(J_{4_{t-2}} + 1)$] in Phase I guppy populations.

Population number	r	Population number	r
1	−0.5166*	6	−0.7704*
2	−.5919*	9	−.6042*
3	−.5215*	10	−.0487
4	−.7300*	11	−.6047*
5	.6158*	12	−.3600

*$P \leq 0.05$.

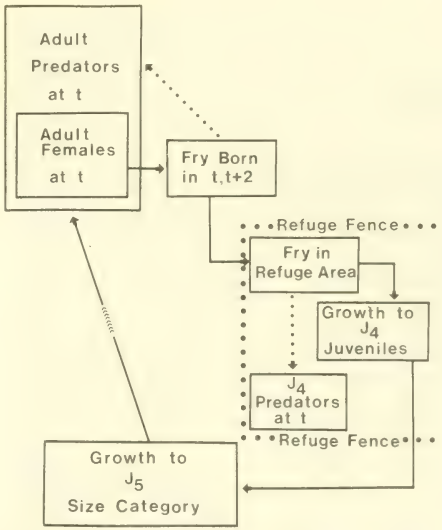


FIGURE 8.—Diagram depicting the hypothesized numerical dynamics model for guppy populations. Solid lines and arrows indicate path from birth to survival as adult. Small dots and arrows depict paths leading to death through cannibalism by adults or juveniles.

OTHER OBSERVATIONS.—Additional data collected during Phase I included examination of guppy scales for fluorescent marks and records of disease incidence. Examination of scales removed from fish at week 36 was disappointing. No scales showed more than five to seven marks while the maximum expected number of marks was nine. It is possible that at the final ration level individual fish did not receive sufficient food intake to produce detectable marks. Further research into the matter was not pursued, but marking was continued during Phase II so that experimental manipulations would remain constant. All guppy disease problems were chronic in nature, minor, and were consistently diagnosed as piscine tuber-

culosis. At no time did deaths due to disease approach epidemic levels in any population. Frequency of disease symptoms, deaths attributable to disease, etc., for each population may be found in Hankin (1978b).

Phase II (Weeks 36-58)

Long-Term Controls: Populations 5, 6, and 12

Total population biomass of control guppy populations during weeks 36-58 confirmed the earlier speculation that populations were near their maximum biomass by week 36. Net changes in total biomass from week 36 to week 58 were +0.5, +0.1, and +0.9 g in populations 5, 6, and 12. Minor asynchronous fluctuations in biomass occurred throughout Phase II in all control populations. Logistic-based estimates of maximum supportable biomass made at week 36 were 30.6, 32.4, and 31.1 g and agreed remarkably well with actual biomass levels at termination, 28.3, 30.7, and 30.7 g.

Control populations showed no signs of convergence in total population numbers nor of parallel fluctuations. Although total numbers in the three control populations differed greatly, total numbers and weights of reproductive females (size categories A_6-A_8) were similar. In populations 5, 6, and 12 there were 37, 36, and 42 such females at termination with corresponding total weights of 20.6, 17.6, and 20.0 g. Since fecundity is roughly proportional to female weight, the three populations had nearly equal reproductive potentials in spite of large differences in total numbers. Adult females accounted for from 57 to 72% of total population biomass. No uniformity in numerical or biomass densities was noted for adult males.

Treated Populations

BIOMASS DYNAMICS.—Total population biomass increased in all treated guppy populations during Phase II (Figure 9). At termination, mean population weights of the three treatment groups were not found significantly different in pairwise comparisons (Student's t tests). Since greatest differences in mean biomass among treatment groups occurred at week 58, there were probably no statistically significant differences in mean biomass throughout Phase II. Alteration of refuge fence spacing had no apparent effect on population biomass growth.

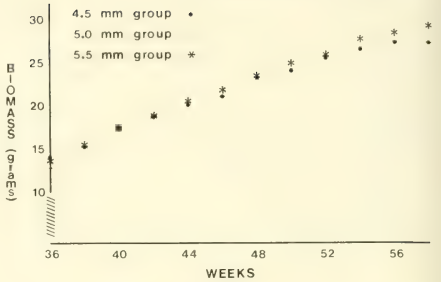


FIGURE 9.—Mean total biomass in treatment groups of guppies during Phase II.

Mean total weights of mature females (size categories A_6-A_8) differed significantly among treatment groups (Student's t tests). The mean percentage of total population biomass accounted for by adult females was consistently higher in the 5.5 mm group (71%) than in the 4.5 mm group (56%).

NUMERICAL DYNAMICS.—Although biomass growth was roughly equal for all treated guppy populations, treatment groups diverged rapidly in total numbers (Figure 10). Smallest population numbers were maintained in the 5.5 mm group, intermediate but highly variable numbers in the 5.0 mm group, and largest numbers in the 4.5 mm group. At termination mean total numbers in the 4.5, 5.0, and 5.5 mm treatment groups were 249, 160, and 128. Mean net additions during Phase II, in the same order, were 172, 86, and 47.

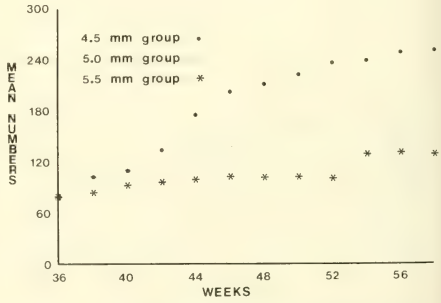


FIGURE 10.—Mean total numbers in treatment groups of guppies during Phase II.

Alteration of refuge fence spacing during Phase II was believed to have influenced both the intensity and duration of juvenile-fry interactions. Behavioral observations of a 5.0 mm refuge population provided a partial explanation of mechanisms involved. A female was observed delivering four fry and the subsequent immediate fate of the fry was followed. Two of the fry were pursued and consumed by two different adult females. Two other fry successfully entered a refuge area after vigorous pursuit by several males and females, including the female giving birth. Once within the refuge area the fry were chased and nipped by larger juveniles. Although the juvenile chase shortly ceased and the fry settled to the aquarium bottom apparently uninjured, alternative outcomes seemed possible. Fry could have been chased outside the refuge area where they would once more be vulnerable to adult predation or the juvenile contact could have resulted in death and perhaps cannibalism. The observations indicated that survival of newly born fry was determined in an extremely short period of time. From release to death or apparent survival in the refuge area never occupied more than perhaps 2 min. Since guppy fry are capable of rapid swimming within minutes after birth, it is unlikely that juvenile pursuit within the refuge area would be successful except during the first few minutes after birth.

The intensity and duration of juvenile-fry interactions, reflected in patterns and magnitude of numerical population growth among treatment groups, was measured and characterized (in parentheses see Table 10) in several ways:

1) by the number of biweekly intervals in which adjusted population increments were ≤ 0 (# PI$\leq$0);
2) by the length in biweekly intervals of the longest period without a positive population increment (Long. 0 PI);
3) by the median adjusted population increment (Med. PI);
4) by the median population numbers (Med. N);
5) by the total number of data observations with zero individuals per any size category (#0/CAT); and
6) by the mean percentage of population numbers in size categories $\geq J_{5.0}$ (% adult).

Measures 1) and 2) were designed to evaluate the prominence of pulsing. Intervals between successive pulses of increase should be greatest when longest periods of juvenile presence occur within refuge areas. The 5.5 mm group should exhibit strong pulsing behavior while the 4.5 mm group should show little if any pulsing (Silliman and Gutsell 1958). Measures 3) and 4) were designed to evaluate effects of juvenile-fry interactions on population numbers. Although the duration of juvenile-fry interactions might not be reflected in total population size at any given time, it should be reflected in median population numbers and in median population increments during the experimental period. Measures 5) and 6) were designed to evaluate size structure smoothness and relative dominance by adults. The characteristic patterns of growth produced under different refuge environments should be reflected in the age structure of treated populations and, although less distinctly, in the size structure. The 4.5 mm group should have a finely graded size structure with juveniles nearly always present, while the 5.5 mm group should have a fluctuating size structure perhaps including distinct "size classes" corresponding to separate pulses of increase.

TABLE 10.—Comparison of measures of numerical population growth for treated guppy populations during Phase II. See text for explanation of column entries.

Treatment group	# PI≤0	Long. 0 PI	Med. PI	Med. N	#0/CAT	% adult
4.5 mm:						
4	1	1	9	192	0	52
7	1	1	22	236	0	41
9	1	1	9	178	0	53
Mean	1	1	13.3	202	0	48.7
5.0 mm:						
1	2	2	21	196	0	47
3	4	1	8	146	0	64
10	4	2	1	83	6	87
Mean	3.3	1.7	10	141.7	2	66
5.5 mm:						
2	4	2	1	99	4	81
8	6	2	0	122	5	73
11	5	4	0	79	12	73
Mean	5	2.7	0.3	100	7	75.7

Comparison of these measures compiled for all treated populations showed clear separation for each measure between 4.5 mm and 5.5 mm groups. In no case was the 5.0 mm group clearly separated from the other groups, although means of all measures for the 5.0 mm group fell between means for 4.5 mm and 5.5 mm groups. Orders of means were in the directions expected on the basis of the juvenile-fry interaction hypothesis (Table 10).

The above comparisons do not, however, allow a "test" for differences in numerical population growth patterns among treatment groups, in part because the several measures are not independent of one another. Rather, comparison of these quan-

titative measures allows qualitative separation of treatment group behavior, illustrates the high variability in behavior within the 5.0 mm refuge fence group, and shows that measures of numerical dynamics generally conform to anticipated differences.

The larger variability in population behavior among the 5.0 mm treatment group was witnessed earlier among the original 10 replicate populations equipped with 5.0 mm refuge fence. Laakso (1959) speculated that the tendency toward cannibalism increased with age of guppies and it may be that at the $J_{4.5}$ stage such tendencies are first beginning to be expressed. The exact age or size at which they become fully expressed may be highly variable. An alternative possibility here would certainly include possible imperfections in refuge fence construction which might have allowed $J_{5.0}$ fish, which clearly exhibited antagonistic behaviors toward fry, to remain within 5.0 mm refuge areas beyond the size at which they should have been excluded.

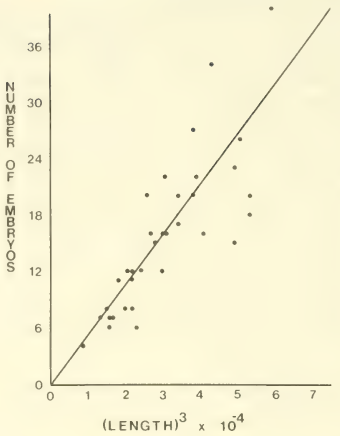


FIGURE 11.—Number of embryos plotted against the cube of female guppy length (standard length in millimeters). Regression line is forced through the origin.

SURVIVAL RATES.—Since the juvenile-fry interactions often created pulses of numerical increase in the guppy populations, there were frequent intervals in which there were no new individuals entering populations. Survival rates for most populations during Phase I and Phase II were estimated by comparing the numbers of fish present at the beginning of such an interval to numbers present at the beginning of the next biweekly interval during which new numerical growth was recorded. Survival rates for the 4.5 mm group and for certain 5.0 mm populations during Phase II could not be estimated due to the continuous nature of numerical increase. Estimates of survival rates for intervals >2 wk were converted to biweekly estimates assuming constant biweekly survival over the longer period. Mean biweekly survival rate estimates ranged from 0.972 to 0.995 during Phase I and from 0.953 to 0.984 during Phase II, averaging 0.984 and 0.970. These biweekly rates indicate roughly 50% annual survival, a reasonable figure for laboratory populations of guppies.

FECUNDITY.—Dissection of a wide size range of gravid guppy females at termination showed that numbers of embryos were linearly related to the cube of female length. Variability in embryo counts appeared to increase with female size (Figure 11). A linear regression of numbers of embryos against the cube of female length was forced through the origin and could be expressed as:

$$E = 5.328\,(L^3 \times 10^{-4})$$

where E = number of embryos
L = standard length in millimeters.

The regression was forced through the origin to ease manipulation of the fecundity relation in further analyses and, over the majority of the size range, did not differ appreciably from a regression with intercept. The empirical relation obtained was similar to earlier results of Felin (1935) and Laakso (1959).

A mean condition factor (K in the formula weight = $K \cdot L^3$) for gravid and nongravid females in $A_{5.5}$ and larger size categories at weeks 36 and 58 was applied to the above relation to obtain an expression relating embryo counts to female weight in grams: $E = 22.347 \cdot$ female weight. In the following analyses the fecundity relation was assumed to have held constant throughout the 58-wk experimental period.

ANALYSIS: NUMERICAL DYNAMICS

Behavior of the treated guppy populations during Phase II generally supported the hypothesis of

juvenile-fry interactions and the proposed conceptual model. However, analysis to this point has implicitly assumed a constant input of newly born fry into the refuge areas, modified downward by the presence of interacting juveniles. Since fry were produced by reproductive females whose numbers and weights increased greatly as populations grew, a complete analysis must clearly include a description of the female reproductive component. Additionally, the influence of adult predators outside the refuge area must be considered. In this section I develop a mathematical model of the dynamics of numerical population change and subject this model to statistical analyses.

Development of a Mathematical Model

Population reproductive potential increases with the weight and number of adult guppy females. The total reproductive potential, i.e., the maximum possible number of fry born in a given interval, in a population at the beginning of an interval can be computed from the fecundity relation and the total female weight as: reproductive potential = $22.347 \cdot \sum_{A_6}^{A_8}$ total weight females per size category. Total reproductive potential is not realized in any given interval since only some (variable) fraction of females will actually deliver broods. In order to obtain estimates of biweekly fry production, the probability that a female will deliver a brood during a 14-d experimental interval is needed.

The calculation of this probability requires: 1) the expected length of an interbrood interval (time from the last brood when the next brood is delivered), 2) an estimate of the gestation period or minimum time between broods, and 3) a frequency distribution for the interbrood interval. In guppies the interbrood interval is roughly 31 d (Breder and Coates 1932; Winge 1937; Rosenthal 1952), gestation period has been estimated at from 21 to 25 d (Winge 1937; Rosenthal 1952), and a rough frequency distribution may be constructed from the preceding studies. Using "renewal process" theory (Drake 1967), the probability that the waiting time Y until the next brood of an individual female is delivered will be ≤14 d (length of a sampling interval), when there is no knowledge of her exact stage in the brood cycle (as was the case for these populations), is denoted by $P(Y \leq 14 \text{ d})$. Letting T = interbrood interval, and s be a fixed but random point in the brood cycle, then $T = s + y$; that is, the total length of the interbrood interval (T) is equal to the time since the last brood (s) plus the waiting time (y) until the next brood is delivered. Using a cumulative density function for the interbrood interval (T), which may be constructed from previous studies, one has (using standard notation):

$$P(T \leq t) = F_T(t).$$

$$\text{Then } f_Y(y) = \frac{[1 - P(T \leq y)]}{E(T)}$$

$$\text{and } P(Y \leq 14) = \int_0^{14} \frac{[1 - P(T \leq y)]}{E(T)}\, dy$$

$$= 1/E(T) \cdot \int_0^{14} [1 - F_T(y)]\, dy \quad (1)$$

where $E(T)$ denotes expected value.

The probability of an interbrood interval of ≤14 d is 0 (gestation period estimates are at least 21 d) so Equation (1) may be reduced to: $P(Y \leq 14) = 14/E(T) = 14/31 = 0.452$.

This probability may be applied to the estimated reproductive potential to obtain an estimate of the expected number of births in a 2-wk interval as: expected number of births $_{t,\, t+2}$ = 0.452 · reproductive potential $_t$. Comparison of adjusted population increments (API) with expected number of births ($\widehat{EB}$) allows estimation of survival rates ($\hat{S}$) for fry born in a given interval as:

$$\hat{S}_{t,\, t+2} = API_{t,\, t+2}\, \widehat{EB}_{t,\, t+2}.$$

Survival of newly born fry through a 2-wk interval depends on both predation by adults outside the refuge area and juvenile-fry interactions within the refuge area. Survival within the refuge area is conditioned upon the event "successful refuge entry," so one has:

$$P(\text{survive to } t+2) = P(A \text{ and } B) = P(A) \cdot P(B \mid A)$$

where $P(A)$ = P("successful refuge entry")
$P(B \mid A)$ = P(survive within refuge area given A has a successful outcome).

Events A and B are related to densities of adults and juveniles, respectively, during a 2-wk interval.

By examination of only those sampling intervals for which the (initial) juvenile ($J_{4.5}$) density equals 0, one may separate the relation between adult density and fry survival from the complicating juvenile-fry interaction. For such intervals, neglecting natural mortality, survival within the refuge area should be approximately 1. That is, when $J_{4.5}$ density = 0: $P(A \text{ and } B) = P(A) = f(\text{adult density only})$. Biweekly fry survival rates were estimated as described above and plotted against numerical densities of fish in size categories $J_{5.0}$ through A_8 in 5.0 mm populations from Phase I and from long-term control populations during Phase II revealing a decreasing trend in survival rates with increasing predator density (Figure 12). Beyond 100 adults, estimated survival was close to zero. The trend appeared roughly exponential (one explanation is based on random encounters between predators and prey, see Ricker 1954), so a negative exponential model was used for further analysis:

$$P(A) = \exp[B_1 \cdot (\text{adult density})]; B_1 < 0.$$

Since adults were always present when juveniles were present in refuge areas, it was not possible to separate the effects of the juvenile-fry interaction from adult predation. By analogy, I also used the negative exponential model to describe the relation between juvenile numbers and refuge area fry survival rates, i.e.:

$$P(B \mid A) = \exp[B_2 \cdot (J_{4.5} \text{ density})]; B_2 \leq 0.$$

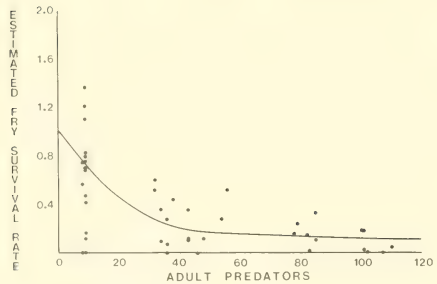


FIGURE 12.—Relation between estimated guppy fry survival rates ($\hat{S}_{t,\,t+2}$) and number of adult guppy predators (number $\geq J_{5.0}$ at t) when no $J_{4.5}$ juveniles were present at t. Line is drawn by eye. Squares represent multiple observations.

The full model appropriate for all sampling intervals is then:

$$P(\text{survive to } t+2 \text{ given born in } t,\, t+2) = \hat{S} = API/\widehat{EB} = \exp(B_1 X_1 + B_2 X_2)$$

where X_1 = number of adults in size categories $J_{5.0}$ and above at time t

X_2 = number of $J_{4.5}$ juveniles at t.

Statistical Analysis

Two techniques were used to fit the collected guppy population data to the proposed model developed above. Both techniques were based on the same assumed model although the model was expressed in different forms according to analysis technique:

$$\hat{S}_{t,\,t+2} = API_{t,\,t+2}/\widehat{EB}_{t,\,t+2} = \exp(B_1 X_{1t} + B_2 X_{2t}), \text{ and} \quad (2)$$

$$API_{t,\,t+2} = \widehat{EB}_{t,\,t+2} \cdot \exp(B_1 X_{1t} + B_2 X_{2t}). \quad (3)$$

Multiple regressions, forced through the origin, were fit to a transformation of Equation (2) (adding 1 unit to API to avoid undefined natural logarithms)[4]:

$$\ln[(API_{t,\,t+2} + 1)/\widehat{EB}_{t,\,t+2}] = \hat{B}_1 X_{1t} + \hat{B}_2 X_{2t}.$$

Alternative estimates of B_1 and B_2, the "coefficients of predation" for adults and juveniles, were obtained by nonlinear least-squares regressions based on a Taylor series linearization of Equation (3) (Draper and Smith 1966). In this case one minimizes:

$$\sum (API_{t,\,t+2} - \widehat{API}_{t,\,t+2})^2 = \sum [API_{t,\,t+2} - \widehat{EB}_{t,\,t+2} \cdot \exp(\hat{B}_1 X_{1t} + \hat{B}_2 X_{2t})]^2$$

to obtain the iterative solutions for B_1 and B_2. Iteration was continued for these estimates until the last estimate agreed with the previous estimate to six decimal places. All population data series were subjected to analysis by the same model. Note that the dependent variable for the

[4]While an interaction term of the form $X_1 X_2$ might seem a logical addition to the above model, analyses failed to indicate that such an interaction was significantly involved in determining numerical dynamics of the populations.

multiple linear regressions is the natural logarithm of estimated survival rates, while for the nonlinear regressions it is actual observed population increments.

If the model were correct one would expect that statistical analyses should give:

1) estimates of the B_1 coefficient similar in all populations,
2) estimates of the B_2 coefficients which are:
   a) close to 0 in the 4.5 mm populations,
   b) some negative number in the 5.0 mm populations,
   c) some negative number larger in absolute value than in b) for 5.5 mm populations.

No juvenile interactions would be expected in the 4.5 mm treatment group and $J_{5.0}$ individuals contributing to predation in the 5.5 mm populations, but not included in X_2, would be expected to increase the B_2 coefficient. Numbers of $J_{4.5}$ individuals present at the beginning of intervals during Phase I were estimated from total numbers and weights recorded for the combined J_4 category monitored during Phase I (see Hankin 1978b for details).

Results of multiple regression analyses of original and long-term 5.0 mm populations appear in Table 11 and of treated populations during Phase II in Table 12. Squared multiple correlation coefficients (r^2), when both adults and juveniles were included in regressions, ranged from 0.8003 to 0.9272 in Phase I populations indicating that about 80 to 90% of the uncorrected sums of squares of the natural logarithms of estimated fry survival rates could be explained by regression on adult and juvenile densities. Estimates of adult predation coefficients were similar for all populations, and estimates of juvenile predation coefficients differed in the expected order among treatment groups. Differences among juvenile predation coefficients were less striking than had been anticipated. Mean estimates of B_2 for 4.5, 5.0, and 5.5 mm treatment groups were -0.0280, -0.1009, and -0.1249.

Alternative estimates of B_1 and B_2, obtained by minimizing the squared deviations between actual and predicted biweekly adjusted popula-

TABLE 11.—Estimates of predation coefficients (B_1, B_2) and squared multiple correlation coefficients (r^2) for Phase I guppy populations. Based on multiple regression analysis of the hypothesized model: $\ln[(API + 1)/\overline{EB}] = B_1X_1 + B_2X_2$. See text for explanation of model parameters.

Population number	Weeks	Fence (mm)	Adults and juveniles			Adults only		Juveniles only	
			B_1	B_2	r^2	B_1	r^2	B_2	r^2
1	0-36	5.0	−0.0471	+0.0055	0.9186	−0.0449	0.9185	−0.1029	0.8423
2	0-36	5.0	−.0426	−.0031	9272	−.0429	.9272	−.1568	.3370
3	0-36	5.0	−.0202	−.1457	.8116	−.0397	.6298	−.2146	.7223
4	0-36	5.0	−.0322	−.0994	9044	−.0448	.8406	−.2292	.6910
5	0-58	5.0	−.0316	−.1485	.8691	−.0512	.8099	−.3084	7661
6	0-58	5.0	−.0221	−.1170	.9111	−.0416	.8580	−.2207	.8576
9	0-36	5.0	−.0472	−.0771	.8324	−.0589	.8080	−.2530	6090
10	0-36	5.0	−.0317	−.1033	.8774	−.0480	.7954	−.2094	.7129
11	0-36	5.0	−.0335	−.1131	.8003	−.0456	6664	−.1943	.5352
12	0-58	5.0	−.0257	−.0963	.8489	−.0347	.8140	−.2637	.6762

TABLE 12.—Estimates of predation coefficients (B_1, B_2) and squared multiple correlation coefficients (r^2) for treated guppy populations during Phase II. Based on multiple regression analysis of the hypothesized model: $\ln([API + 1]/\overline{EB}) = B_1X_1 + B_2X_2$. See text for explanation of model parameters.

Population number	Weeks	Fence (mm)	Adults and juveniles			Adults only		Juveniles only	
			B_1	B_2	r^2	B_1	r^2	B_2	r^2
4	36-58	4.5	−0.0155	−0.0665	0.9005	−0.0328	0.8850	−0.1225	0.8888
7	36-58	4.5	−.0176	−.0253	.8529	−.0250	.8385	−.0755	.7852
9	36-58	4.5	−.0303	+.0079	.8867	−.0288	.8864	−.1340	.8047
Means: 4.5 mm group			−.0211	−.0280	8800	−.0289	.8700	−.1107	.8262
1	36-58	5.0	−.0068	−.1228	.8744	−.0282	.8567	−.1608	.8727
3	36-58	5.0	−.0276	−.0682	.9211	−.0375	.9078	−.2258	.8352
10	36-58	5.0	−.0492	−.1117	.9501	−.0538	.9437	−.7307	.5749
Means: 5.0 mm group			−.0270	−.1009	.9152	−.0398	.9027	−.3724	.7609
2	36-58	5.5	−.0392	−.1433	9599	−.0518	.9532	−.2274	.9078
8	36-58	5.5	−.0430	−.0417	.9550	−.0486	.9536	−.1732	.8999
11	36-58	5.5	−.0450	−.1896	.9114	−.0589	.8617	−.3131	.8057
Means: 5.5 mm group			−.0424	−.1249	.9421	−.0531	.9228	−.2546	.8711

tion increments, were strikingly different among treatment groups. Mean estimates of B_2 in 4.5 mm and 5.0 mm treatment groups were -0.0024 and -0.0857. Estimates for the three 5.5 mm populations were -0.0494, -0.1523, and "$-$. Large" (fails to converge to finite negative number), again indicating strong interaction by juveniles (Table 13). However, alternative fits of actual population increases against adult and juvenile densities could account for an average of only 59% of the variation in the uncorrected sums of squares of the adjusted population increment variable. Still, given initial population states at the beginning of intervals, the patterns of predicted increments exhibited pronounced pulses and generally behaved well relative to actual population histories (Figure 13).

TABLE 13.—Estimates of predation coefficients (B_1 and B_2) and squared multiple correlation coefficients (r^2) for all treated guppy populations for specified intervals. Based on iterative Taylor Series approximation analysis of the hypothesized model: $API = \widehat{EB} \times \exp(B_1X_1 + B_2X_2)$. Estimates which fail to converge (−.Large) are not included in means.

Population number	Weeks	Refuge (mm)	B_1	B_2	r^2
1	0-36	5.0	−0.0258	−0.0224	0.8286
2	0-36	5.0	−.0340	−.0137	.7364
3	0-36	5.0	−.0172	−.1972	.5295
4	0-36	5.0	−.0223	−.1290	.7867
5	0-58	5.0	−.0636	−.4198	.4000
6	0-58	5.0	−.0184	−.1354	.4997
9	0-36	5.0	−.0509	−.0640	.2900
10	0-36	5.0	−.0346	−.0585	.6453
11	0-36	5.0	−.0195	(−.Large)	.7671
12	0-58	5.0	−.0204	−.1137	.4270
Means: Phase I and long-term controls—5.0 mm			−.0307	−.1282	.5461
4	36-58	4.5	−.0267	−.0025	.6519
7	36-58	4.5	−.0181	−.0088	.8022
9	36-58	4.5	−.0284	+.0041	.7512
Means: 4.5 mm group			−.0244	−.0024	.7351
1	36-58	5.0	−.0120	−.0717	.8459
3	36-58	5.0	−.0286	−.0367	.7236
10	36-58	5.0	−.0484	−.1487	.4371
Means: 5.0 mm group			−.0297	−.0857	.6689
2	36-58	5.5	−.0367	−.1523	.5103
8	36-58	5.5	−.0355	−.0494	.5890
11	36-58	5.5	−.0246	(−.Large)	.6060
Means: 5.5 mm group			−.0323	−.1009	.5684

DISCUSSION

In no earlier population experiments with guppies have detailed analyses of numerical population growth been attempted. Analyses employed in this study were designed with two purposes in mind. Comparisons of numerical dynamics measures, while perhaps unsatisfying to those demanding rigorous statistical tests or parameter estimates, allowed qualitative distinctions to be drawn among treatment groups and

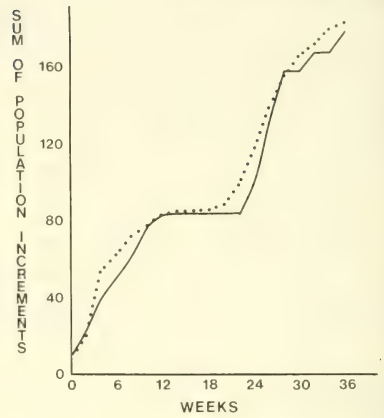


FIGURE 13.—Sum of observed (solid line) and predicted (dots) population increments for guppy population 4 during Phase I.

showed clear differences in the patterns and variability of numerical population growth. Least-squares regression techniques, while shedding no light on the qualitative features of numerical increase, allowed evaluation of the fit of the hypothesized numerical dynamics model to collected experimental data and also allowed estimation of adult and juvenile stock predation coefficients. That multiple regression analysis failed to indicate as striking differences in juvenile predation coefficients among treatment groups as did nonlinear least-squares regression illustrates a strong relation between analysis technique and analysis result. Clearly, parameter estimates based on linear fits of a survival equation are not comparable with those obtained by minimizing squared deviations between observed and predicted population increments, although the underlying numerical dynamics model and experimental data used are identical for both analyses. In the absence of detailed data specifying the true error component of the underlying model it is unclear which regression technique is appropriate. Regardless of such technical issues, all analyses support the hypothesis that alteration of refuge habitat quality may significantly change biological interactions among components of a population. This finding is compatible with earlier studies and also unifies the "conflicting" results of previous studies with and without refuge areas.

Analyses of these experimental populations show that there are two distinctly different components of experimental population growth and that these two components should be separated in mathematical treatments of population dynamics. Numerical growth in experimental populations is an extremely variable population phenomenon, only weakly predictable through convential models and statistical techniques. Total biomass growth is a relatively invariant population process, highly predictable, and nearly immediately responsive to slight disturbances in food supply. From a modeling perspective, these considerations imply that population biomass growth might be adequately described by a simple deterministic model, such as logistic growth, while description of numerical growth may require more complex and perhaps stochastic models.

Description of numerical dynamics is, of course, the province of stock-recruitment theory. Neglecting the issue of the extreme variability in numerical behavior of these populations for the moment, these experiments reveal at least two likely biological complications which may render simple stock-recruitment theory of limited practical application. The observed strong juvenile-fry interaction shows that recruitment may depend not only on parent adult stock but also on juvenile stock, perhaps at different times and in different places. Simple stock-recruitment theory clearly requires modification to account for such interactions. Also, density-dependence of growth may further compound the complexity of the recruitment process. While numerical change within sampling intervals may be adequately, although imperfectly, described by the model developed, eventual recruits, say in terms of adult females, are evidently not a simple fraction of numerical increase some fixed number of weeks previous. Models of recruitment in fish populations have not explicitly dealt with complications that might be introduced by the density-dependence of year-class growth, dependence that may occur after a year class has been established.

The probable general effects of a strong juvenile-fry interaction may be examined by making a few simplifying assumptions (none of which are more than only approximately met by guppies) and then to recast the experimental numerical dynamics model as a more general relation similar in form to the simple stock-recruitment model first proposed by Ricker (1954). These assumptions are: 1) The expected number of births is proportional to the number of reproductive females rather than to the biomass of females. 2) The number of reproductive females is proportional to the total number of adult predators. 3) The correlation between size and age is perfect and growth rates of individuals are density independent. Then, letting A = number of adult predators, J = number of interacting juveniles, and a, b_1, b_2 = constants, the experimental numerical dynamics model,

$$API = \widehat{EB} \cdot \exp(B_1 X_1 + B_2 X_2),$$

may be reexpressed as (using assumptions 1) and 2)):

$$API = a A \exp(b_1 A + b_2 J)$$

and if recruits are a constant fraction of numerical increase in a given period (using assumption 3)):

$$R = a' A \exp(b_1 A + b_2 J)$$

where a' = constant
R = "recruitment."

Three dimensions are required for visualization of a hypothetical stock-recuitment relation incorporating a juvenile-fry interaction. To examine such a relation, experimental estimates of b_1 (-0.031) and of b_2 (-0.160) were taken from the mean nonlinear estimates for 5.0 mm refuge fence populations. Based on ratios of expected number of births to numbers of adult predators, a rough estimate for a' was obtained ($= 2$) by assuming that recruitment was determined at the end of a sampling period. A plot of the adult-juvenile stock-recruitment relation thus produced is given in Figure 14.

There is a pronounced flattening of the recruitment surface with increasing juvenile density. At high juvenile density (15 on the graph), recruitment is low, nearly constant, and is essentially independent of adult stock. If such interactions occur within populations of fish simple plots of recruitment against adult stock would reveal little trend at high juvenile densities. At low juvenile densities, however, recruitment appears strongly related to adult stock in the classic dome-shaped manner. At low levels of adult stock recruitment may fluctuate considerably, independent of adult stock, as a response to high or low juvenile densities. In general the more intense the inhibition of fry survival rates by juveniles, the

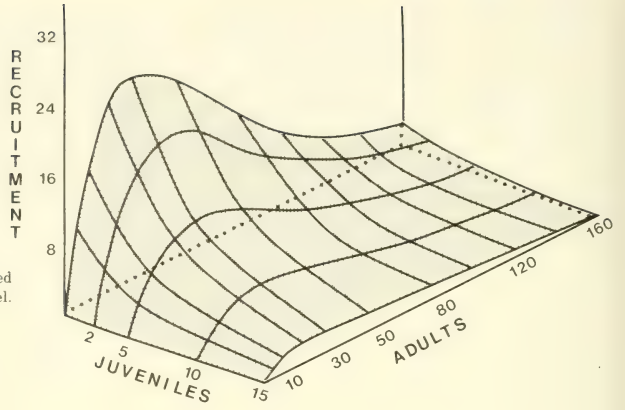


FIGURE 14.—Visualization of proposed adult-juvenile stock-recruitment model. See text for explanation.

more extreme would be the expected fluctuations in recruitment at the same adult stock densities. Variability in recruitment would be increased with a decrease in adult stock, as would be caused by fishing.

If, instead of juveniles of the same species, juveniles (or perhaps adults) of another species interact with fry (or larvae) in a similar manner, one may begin to imagine the complexity of possible "true" recruitment mechanisms in fish populations. Standard simple stock-recruitment relations may require more dependence of recruitment on adult stock alone than is justified. Intraspecific or interspecific interactions of the type observed in these experimental populations clearly create complex recruitment processes, incapable of even approximate description on the basis of adult stock alone. If recruitment theory is to be of practical significance in the management of fish populations, it seems that the numerical dynamics of given populations will have to be examined as unique biological phenomena, perhaps only rarely susceptible to standardized mathematical descriptions such as the Ricker stock-recruitment model.

One may, of course, deny the relevance of the above conclusions, derived from single species laboratory populations maintained under fixed food supply, for the modeling of natural populations. In particular, it may be questioned whether the extreme variability in numerical population growth observed in experimental populations does in fact also occur in natural populations. And it may also be questioned whether natural populations actually exhibit such extreme response of individual growth rates to variations in population density. Several aspects of guppy life history and empirical observations from natural populations together argue that experimental variation in numerical population growth indeed has clear parallels in natural populations. The second issue, that concerning density dependence of growth, is less easily resolved.

The extreme variability in numerical population growth observed in these experimental populations arises primarily from small population size. This variation is inherent and depends on the guppy reproductive cycle. Since all statistical analyses were based on expectations of events, and since in small populations the discrepancy between actual outcomes of events and their expectations may be large, statistical analysis and prediction of numerical growth patterns were inherently weak. For example, fry survival rate estimates were based on the expected number of births in a 2-wk interval rather than on actual births which were unknown. At initiation of populations only five adult females were present. The initial "biweekly" sampling interval was 16 d so the probability of an individual female delivering a brood within the first interval was $16/31 = 0.516$. Since broods of females are delivered independently of one another, one may reasonably assume that the number of broods delivered in the first interval among five adult females was binomially distributed with parameters n (= 5) and

p (= 0.516). The mean of this distribution, $n \cdot p$, is the expected number of broods delivered in the first period, or: 5 × 0.516 = 2.58 broods.

Further, taking the mean initial weight of adult females to be 0.5 g, the fecundity relation predicts an expected brood size of 11.14 fry and a possible range of from 5 to perhaps 20/brood. Thus, the expected number of births (EB) is: 2.58 broods × 11.14 births/brood = 28.73 births = $n \cdot p \cdot u$ where: u = expected outcome of a success (i.e., expected number per brood). But the range of possible values for the random variable "number of births in a biweekly interval" was from 0 (0 broods × 5 births/brood) to 100 (5 broods × 20 births/brood) births. Assuming that perhaps 70% of the fry born in the first interval survived, since adult predator densities were very low, the collected statistic API could have had a range from 0 to about 70. Hence the estimated fry survival rates could have had a range of from 0 (API/EB = 0/28.73), had no broods been delivered, to as high as 2.44 (70/28.73), if all five females delivered broods. Estimated fry survival rates at adult densities of eight or nine during the first 4 wk reflected this possible variation in actual numbers of broods delivered and number of births per brood and ranged from 0 to 1.38. Thus large variation among estimated fry survival rates at low adult densities is possible and unavoidable if the actual number of births is unknown.

In natural populations fluctuations in year-class strength, the natural analog to numerical experimental population increase, due to variation in early life survival, often range over two orders of magnitude (Forney 1976). While the primary causes behind such variations (often at the same or similar stock densities) seem to be usually environmental, unlike experimental populations under controlled conditions, this variation seems at least equal to that observed in these experiments. Guppy reproductive features, including small brood size, very high but variable fry survival, and high variability in timing of brood delivery, are replaced in most natural fish populations by high fecundity and extremely low and variable early life survival. Thus, although underlying causes differ markedly, observed fluctuations in numerical population growth of natural populations at least equal those observed in experimental populations.

The striking density dependence of growth observed in these populations may, however, represent an exaggeration of probable levels of growth response to density that may exist in natural populations. Many natural populations are probably not directly limited by their food supply, but rather by competing species, suitable habitat for all life stages, and/or harvest by man. Natural population biomass may in general fall below that which the underlying food supply could in theory support. Also, variation in food supply would make field observations of density-dependent growth less striking. Finally, empirical observations suggest that such intense growth depression with high population density is rarely a feature of commercial fish populations. Rather, observations of extreme stunting of fish size have been collected from simple single species populations in many respects analogous to the experimental populations. Stunting among high density pond and small lake populations of yellow perch, *Perca flavescens*, and eastern brook trout, *Salvelinus fontinalis*, is well known. Although extreme density dependence of growth does occur in natural populations, it seems unlikely for most exploited populations, especially when population biomass has been reduced to perhaps one-half of unexploited levels.

SUMMARY

The ultimate interest in laboratory study of the stock-recruitment process is to gain insight into this fundamental problem and to apply such insight to the study and modeling of natural populations. These experiments illustrate that the stock-recruitment process may involve more than a single adult stock-related feedback control and that more complex mechanisms may involve interactions among several stock components. While mathematical models of more complex stock-recruitment processes may be constructed, that such complex analytic models may be usefully applied in practice is far from clear. Two serious application problems exist and these problems seem inherent to analysis of stock-recruitment relations for any temperate species. The time frame and economic expense necessary to collect data suitable for statistical analysis of possible complex stock-recruitment models and the probably inherent variability of the recruitment process argue that if, indeed, such complex models are to be of practical use, major rethinking of analysis and data collection approaches is required.

Data collection during these experimental stud-

ies, which allowed eventual crude prediction of numerical population behavior, might be roughly analogous to the following field data collection: 1) Collecting data on at least adult stock, young-of-year, and yearling densities from 10 fish populations of the same species in similar environments for 18 yr each. 2) Restructuring refuge area habitats for six of the similar populations, perhaps by removing or increasing weed cover, dramatically reducing the size of all populations, and collecting appropriate data for an additional 11 yr. Few fishery investigators have the opportunity to carry out such an "experiment" in a field context. Instead, a single population may be studied, under fortunate circumstances, for perhaps one or two decades. Analogous replication is impossible. Since the investigator is (usually) not allowed to actively manipulate population age or size structure, but must instead maintain a passive observer role, data collected in a decade might cover only a small range of juvenile and/or adult stock sizes. Recruited year classes, exposed to perhaps violent fluctuations in environmental factors influencing early life survival, might rarely give any indications of a dependency of recruitment on adult or juvenile densities in previous years.

Faced with such constraints on data collection, there seem possible several constructive alternative responses. The general passive approach may be neither appropriate nor effective, and active (experimental) manipulation of populations, forcing collection of data not otherwise obtainable, may be required. This approach has been advocated by Walters and Hilborn (1976) although it clearly calls for major rethinking of the fishery biologist's role. Second, it is possible that year-class strength and adult and other stock components during past years may be estimated through data extraction techniques based on simple gross population measures, e.g., from total biomass harvested from commercial species (Walter and Hoagman 1975). Thus, rather than bemoaning the slow pace at which future observations may be gathered, one may consider past fishery data as an untapped reservoir of information suitable for analysis of the dynamics of recruitment. Statistical evaluation of relations among such extracted estimates does, however, raise serious analytic and philosophic issues. Finally, comparative study of year-class fluctuations among related species and fisheries holds far more promise for revealing biological mechanisms underlying recruitment than is indicated by published literature (Regier 1978).

Since there may be constructive responses to data collection problems, the probably inherent high variability of the stock-recruitment process causes the author greater concern. Although the impact of specific environmental factors may occasionally be separated from possible internal biological controls (Nelson et al. 1977) and allow reduction of unexplained variation in year-class strength, it seems unlikely that a single environmental variable regularly exerts significant impact on year-class strength. Thus, while apparent variation in year-class strength may be reduced under fortunate circumstances, either by accounting for environmental impacts or by considering all relevant stock components, it seems unlikely that collected data will ever fall neatly along some theoretical curve or surface. In general, expectations for statistical measures of goodness of fit for stock-recruitment relations are probably grossly unrealistic and poor fits should be expected. How one ought to evaluate empirical stock-recruitment fits, when the appropriate standard for comparison is probably not "100% of variation" or a correlation of 1, is not clear, although attention has already focused on optimal use of unreliable stock-recruitment parameter estimates (Walters 1975). The danger of presuming independence of recruitment and population stock components, however, seems far more severe than are errors of estimation and generally unsatisfying statistical analyses.

It is hoped that the results of these experiments and the demonstration of a complex multistage recruitment process will stimulate renewed interest in study of the possible biological determinants of recruitment. That simple stock-recruitment theory may often be biologically inappropriate seems clear. But whether more complex and more biologically realistic models of recruitment processes, with their further demands for data collection, will prove of practical use seems far from clear. In the author's view, at present, a wide gulf separates stock-recruitment theory from practice. More careful consideration of the practical use of this body of theory and more realistic expectations from its use are required if the theory is to achieve its proper role in fishery management.

ACKNOWLEDGMENTS

My deep appreciation is given to the many

Cornell faculty and staff who contributed to this research. Louis Leibovitz performed needed pathological examinations of fish and the Levine Laboratory for Avian and Aquatic Animal Medicine allowed access to their fluorescence microscope. Alfred Eipper, former Leader, New York Cooperative Fishery Research Unit, purchased and loaned the analytical balance which enabled accurate measurements of weight. Douglas Robson, Biometrics Unit, and William Youngs, Natural Resources, provided invaluable criticism, encouragement, and moral support throughout the research. Edward Raney, President, Ichthyological Associates, is thanked for his support of the graduate program in Natural Resources and Harry Everhart, Chairman, for considering me worthy of this support. Thanks are also extended to James Zweifel, Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, for his perceptive review of an earlier draft, and the final paper contents reflect his significant contributions.

LITERATURE CITED

BERTALANFFY, L. VON.
1938. A quantitative theory of organic growth (Inquiries on growth laws. II). Hum. Biol. 10:181-213.

BEVERTON, R. J. H., AND S. J. HOLT.
1957. On the dynamics of exploited fish populations. Fish. Invest. Minist. Agric. Fish. Food (G.B.), Ser. II, 19, 533 p.

BREDER, C. M., JR., AND C. W. COATES.
1932. A preliminary study of population stability and sex ratio of *Lebistes*. Copeia 1932:147-155.

BUTLER, T. H.
1961. Growth and age determination of the Pacific edible crab *Cancer magister* Dana. J. Fish. Res. Board Can. 18:873-891.

DRAKE, A. W.
1967. Fundamentals of applied probability theory. McGraw-Hill, N.Y., 283 p.

DRAPER, N. R., AND H. SMITH.
1966. Applied regression analysis. Wiley, N.Y., 407 p.

FELIN, F.
1935. On reproduction and growth in the viviparous Poeciliid *Lebistes reticulatus* (Peters). Masters Thesis, Leland Stanford Junior Univ., Palo Alto, Calif.

FORNEY, J. L.
1976. Year-class formation in the walleye (*Stizostedion vitreum vitreum*) population of Oneida Lake, New York, 1966-73. J. Fish. Res. Board Can. 33:783-792.

GOTSHALL, D. W.
1978. Relative abundance studies of Dungeness crabs, *Cancer magister*, in Northern California. Calif. Fish Game 64:24-37.

GULLAND, J. A.
1962. The application of mathematical models to fish populations. *In* E. D. Le Cren and M. W. Holdgate (editors), The exploitation of natural animal populations, p. 204-217. Blackwell Sci. Publ., Lond.

HANKIN, D. G.
1978a. New fluorescent fish scale marker. Prog. Fish-Cult. 40:163-164.
1978b. Stock and recruitment in laboratory fish populations. Ph.D. Thesis, Cornell Univ., Ithaca, 186 p.

HESTER, F. J.
1964. Effects of food supply on fecundity in the female guppy, *Lebistes reticulatus* (Peters). J. Fish. Res. Board Can. 21:757-764.

LAAKSO, M.
1959. The influence of population density and harvesting techniques on growth of the common guppy *Lebistes reticulatus*. Ph.D. Thesis, Univ. Minnesota, 123 p.

MAY, R. M.
1975. Biological populations obeying difference equations: Stable points, stable cycles, and chaos. J. Theor. Biol. 51:511-524.

MCKELVEY, R., D. G. HANKIN, K. YANOSKO, AND C. SNYGG.
In press. Stable cycles in multi-stage recruitment models: An application to the Northern California Dungeness crab fishery. Can. J. Fish. Aquatic Sci. 37(12).

NELSON, W. R., M. C. INGHAM, AND W. E. SCHAAF.
1977. Larval transport and year-class strength of Atlantic menhaden, *Brevoortia tyrannus*. Fish. Bull., U.S. 75: 23-41.

OSTER, G.
1975. Stochastic behavior of deterministic models. *In* S. A. Levin (editor), Ecosystem analysis and prediction, p. 24-37. Soc. Ind. Appl. Math., Phila.

PURSER, G. L.
1938. Reproduction in *Lebistes reticulatus*. Q. J. Microsc. Sci. 81:151-157.

REGIER, H. A.
1978. A balanced science of renewable resources with particular reference to fisheries. Wash. Sea Grant Publ. WSG 78-1, 108 p.

RICKER, W. E.
1954. Stock and recruitment. J. Fish. Res. Board Can. 11:559-623.

ROSENTHAL, H. L.
1952. Observations on reproduction of the Poeciliid *Lebistes reticulatus* (Peters). Biol. Bull. (Woods Hole) 102:30-38.

ROYAMA, T.
1977. Population persistence and density dependence. Ecol. Monogr. 47:1-35.

SHOEMAKER, H. H.
1944. A laboratory study of fish populations. Trans. Am. Fish. Soc. 74:350-359.

SILLIMAN, R. P.
1948. Factors affecting population levels in *Lebistes reticulatus*. Copeia 1948:40-47.
1968. Interaction of food level and exploitation in experimental fish populations. U.S. Fish Wildl. Serv., Fish. Bull. 66:425-439.

SILLIMAN, R. P., AND J. S. GUTSELL.
1958. Experimental exploitation of fish populations. U.S. Fish Wildl. Serv., Fish. Bull. 58:215-252.

TURNER, C. L.
1937. Reproductive cycles and superfetation in poeciliid fishes. Biol. Bull. (Woods Hole) 72:145-164.

WALTER, G., AND W. J. HOAGMAN.
1975. A method for estimating year class strength from abundance data with application to the fishery of Green Bay, Lake Michigan. Trans. Am. Fish. Soc. 104:245-255.
WALTERS, C. J.
1975. Optimal harvest strategies for salmon in relation to environmental variability and uncertain production parameters. J. Fish. Res. Board Can. 32:1777-1784.
WALTERS, C. J., AND R. HILBORN.
1976. Adaptive control of fishing systems. J. Fish. Res. Board Can. 33:145-159.
WARREN, E. W.
1973. The establishment of a 'normal' population and its behavioural maintenance in the guppy—*Poecilia reticulata* (Peters). J. Fish Biol. 5:285-304.
WINGE, O.
1937. Succession of broods in *Lebistes*. Nature (Lond.) 140:467.
YAMAGISHI, H.
1976. Experimental study on population dynamics in the guppy, *Poecilia reticulata* (Peters). Effect of shelters on the increase of population density. J. Fish Biol. 9:51-65.

DISTRIBUTION AND ABUNDANCE OF *HALOBATES* SPECIES (INSECTA: HETEROPTERA) IN THE EASTERN TROPICAL PACIFIC

LANNA CHENG[1] AND ERIC SHULENBERGER[2]

ABSTRACT

Halobates specimens were sorted from 1,649 surface neuston samples collected from the eastern tropical Pacific Ocean. At least one specimen was captured in each of 498 samples. Only 34 samples contained more than one species of *Halobates*. Four species, *H. micans*, *H. sobrinus*, *H. sericeus*, and *H. splendens*, were found in the eastern tropical Pacific area. The abundance estimates (lower bounds) range from 400 to 10,000 per km^2. Detailed zoogeographical distributions of the four species are presented. *Halobates micans* is a warmwater cosmopolite found between lat. 20° N and 20° S; *H. sericeus* appears to be confined to the central watermasses of the North and South Pacific and does not occur in the zonal equatorial currents; *H. sobrinus*, the most abundant of the four, is confined to the equatorial upwelling regions off the west coast of Central America; and *H. splendens*, the rarest species, appears to be associated with the central South Pacific watermass or the South American west coast current system. Although there is considerable overlap in the absolute geographical ranges of the three more abundant species, the regions in which they are abundant are almost entirely separate. Whether this is due to biological or physical processes is unknown.

Five species of the genus *Halobates* Eschscholtz (Insecta, Heteroptera: Gerridae), popularly called marine "water striders" or "sea skaters," are the only known insects whose normal habitat is the high seas. These pelagic insect plankters occupy an unique, truly two-dimensional environment. They are not known to penetrate below or rise above the surface (no winged forms are known for any *Halobates* species; Cheng and Fernando 1969). *Halobates* spp. spend their entire life cycle at the air-sea interface, and may therefore provide us with an unique opportunity to use them as biological tools for investigating air-sea and surface phenomena.

The peculiar habitat of oceanic *Halobates* spp. precludes their capture (except accidentally) by standard zooplankton or water-sampling equipment, and presents interesting questions of zoogeography and in the evolution of species. The occasional oceanic *Halobates* specimens found in conventional plankton samples made with submerged nets have shown that the five oceanic species are widely distributed on a scale of ocean-basin magnitude (Herring 1961; Savilov 1967; Scheltema 1968; Cheng 1973a, 1974). Although the ranges of distribution of the Pacific *Halobates* spp. have been broadly defined by Savilov (1967), there have been few data for these insects from the southeastern Pacific; furthermore, no detailed quantitative study has hitherto been made on the sea skaters in the Pacific Ocean. An unique series of surface samples collected during the EASTROPAC survey enabled us to carry out an extensive study of *Halobates* spp. in the eastern tropical Pacific Ocean. We present here a detailed description of mesoscale (several hundreds of kilometers) zoogeographic patterns of four *Halobates* spp. in the area, as well as information on abundance, cooccurrence of species, and temperature effects on occurrence of species.

Various aspects of the biology of *Halobates* spp. are described in the literature. The taxonomy of the genus is reasonably well understood (Herring 1961). All 42 species described are to some extent associated with saltwater—mostly brackish waters or nearshore marine habitats. Some are confined to island groups or nearshore lagoons, estuaries, or bays (Cheng 1973a; Andersen and Polhemus 1976). Only five *Halobates* species (*H. micans* Eschscholtz, *H. sericeus* Eschscholtz, *H. sobrinus* White, *H. splendens* Witlaczil, and *H. germanus* White) are truly high-seas animals. Special adaptations of pelagic *Halobates* to its peculiar habitat include: 1) an ability to lay eggs on flotsam (Cheng 1974); 2) a cuticle with a microhair layer which traps air and prevents the

[1]Scripps Institution of Oceanography, University of California, La Jolla, CA 92093.
[2]San Diego Natural History Museum, P.O. Box 1390, San Diego, CA 92112.

Manuscript accepted February 1980.
FISHERY BULLETIN: VOL. 78, NO. 3, 1980.

insects from being wetted by rain, spray, waves, and accidental submergence (Cheng 1973b; Andersen 1977); 3) a highly UV-absorbent cuticle, presumably to prevent chromosomal damage (Cheng et al. 1978); and 4) an ability to store relatively large amounts of food as triglycerides which their brackish-water and freshwater relatives are not known to possess (Lee and Cheng 1974). To date, attempts to rear pelagic *Halobates* in the laboratory have failed. Our knowledge of these insects is thus based upon analyses of preserved samples and on short-term observations or experiments carried out at sea. The present data are from an extensive set of neuston samples taken during the EASTROPAC investigations, which allows us to examine some aspects of species distribution and cooccurrence in relatively fine spatial detail.

METHODS

Present samples were collected during the EASTROPAC project, which surveyed the eastern Pacific between lat. 20° N and 20° S from the west coast of the American continents to about long. 120° W. There were seven cruises between January 1967 and April 1968, each of about 2-mo duration. Figure 1 presents areas surveyed for most of these cruises; some cruise tracks were complex, and areas surveyed and cruise length differed from cruise to cruise: details of cruise tracks are available (Fishery-Oceanography Center,[3] and figures 10-70 TC in Love 1972 [EASTROPAC Atlas, Vol. 1]). The results of some of the biological, chemical, physical, and meteorological measurements have been published in several EASTROPAC Atlases (Love 1970-75) and elsewhere (Ahlstrom 1971, 1972; Tsuchiya 1974).

The neuston nets used to collect our samples filter only the top few centimeters of water, but may occasionally skip out of the water ("porpoising"; see Cheng 1975a). Moreover, to some extent, *Halobates* is able to detect and avoid such a net both visually (Cheng 1973c; Cheng and Enright 1973) and by receiving tactile warnings of its approach (Wilcox 1972). Consequently, the samples yield at best only semiquantitative data on *Halobates* and other pleustonic organisms (Cheng 1975a).

All the samples were replicates; a 505 μm mesh net with a circular mouth 1 m in diameter was towed half submerged at about 3 kn (≈ 1.5 m/s) for 20 min. Optimally, such a tow sweeps a path 1 m wide and 1,800 m long. Abundance of *Halobates* spp. is treated as number of individuals caught per standard tow; such a tow covers an area of about 1,800 m^2. However, our use of 1,800 m^2 as the "area per tow" is conservative, because both porpoising and variable depth of submergence will decrease the actual area covered. Possible avoidance by *Halobates* makes our abundance estimates even more conservative. Samples were preserved in 70% ethanol. Of 1,649 surface samples, 498 contained at least one *Halobates* individual. A total of 3,236 individuals were identified to species (Cheng 1975b). For each sample, we recorded the number of adults and nymphs; nymphs were identified to developmental stage and final instar nymphs and adults were sexed. Detailed information on the cruise series, the total number of surface tows made during each cruise, and the number of positive tows (i.e., containing *Halobates*) are presented in Table 1.

TABLE 1.—EASTROPAC cruise series, number of surface tows made, and number of tows containing *Halobates* spp. (1967-68).

Cruise		No. surface tows	
Series number	Inclusive dates	Total	With *Halobates* spp.
11	24 Jan.- 6 Mar.	120	67
12	7 Feb.-24 Mar.	118	41
13	20 Jan.-31 Mar.	141	42
14	21 Jan.-10 Apr.	98	25
20	10 Apr.-31 May.	128	52
30	14 June- 2 Aug.	127	26
47	31 July-29 Sept.	156	24
45	3 Aug.-25 Sept.	85	32
50	16 Oct.- 3 Dec.	120	36
OP[1]	13 Nov.- 2 Dec.	49	9
60	18 Dec.- 5 Feb.	124	31
76	19 Feb.- 5 Apr.	101	40
77	20 Jan.-28 Apr.	157	39
75	15 Feb.-15 Apr.	125	34

[1]First digit of cruise number denotes the series, except for *Oceanographer* which is a "ship of opportunity" used in series 50.

RESULTS AND DISCUSSION

Species Distributions

Worldwide distributions of oceanic *Halobates* spp. have been presented by Herring (1961), Savilov (1967), and Cheng (1973a, 1974). Updated worldwide distributions of the four oceanic species which occur in the EASTROPAC area are shown in Figure 2. The general distribution of *Halobates* spp. resembles known large-scale plankton dis-

[3]Fishery-Oceanography Center. 1966-69. EASTROPAC Information Paper no. 1-11 (available from National Marine Fisheries Center, P.O. Box 271, La Jolla, CA 92038).

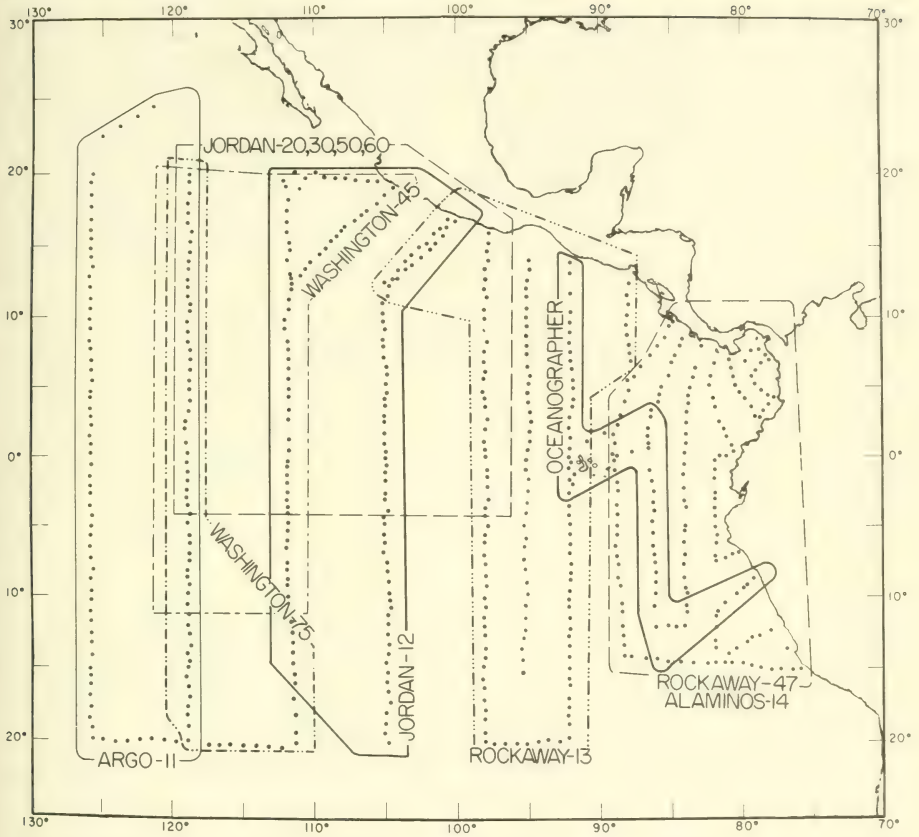


FIGURE 1.—General cruise tracks for the EASTROPAC Investigation showing basic station positions and areas covered during each cruise. Detailed data given in Table 1; exact station positions differ slightly from cruise to cruise.

tribution patterns, e.g., the eastern tropical Pacific, transition zone, central watermass, warmwater cosmopolite, and equatorial distributional patterns found by McGowan (1971, 1974), Reid et al. (1978), and Brinton (1979). These patterns seem to parallel the general surface circulation of central gyres, equatorial zonal flows, and eastern-boundary upwelling areas at the Equator (Sverdrup et al. 1942). No *Halobates* spp. is known to occur regularly at high latitudes.

Halobates micans is clearly a cosmopolitan tropical species occurring in all the world's equatorial current regions (Figure 2). Specimens occur at latitudes higher than about 40° (lat. 55° S, long. 45° W and lat. 52° N, long. 36° W in Figure 2a) only where poleward extensions of strong warm surface currents are known (e.g., Gulf Stream and Kuroshio).

The North and South Pacific central gyres and the South Atlantic central gyre do not appear to contain *H. micans* in contrast to the North Atlantic central gyre (Figure 2). The central North Atlantic is more heavily sampled than any of the other three gyres; however, there are hydrogaphic reasons to believe that the results are valid, independent of sampling density. The Gulf Stream

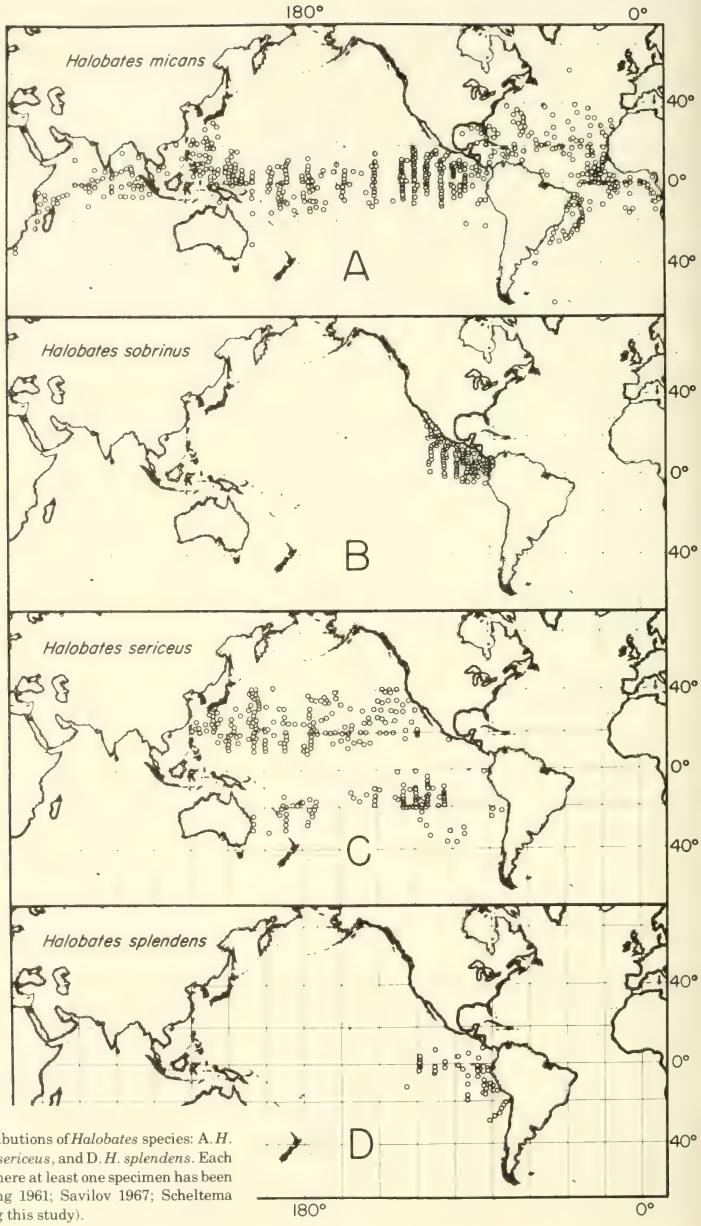


FIGURE 2.—Worldwide distributions of *Halobates* species: A. *H. micans*, B. *H. sobrinus*, C. *H. sericeus*, and D. *H. splendens*. Each circle represents a position where at least one specimen has been collected. (Data from Herring 1961; Savilov 1967; Scheltema 1968; Cheng 1974; and Cheng this study).

produces cold core "rings" of water which migrate into the central North Atlantic watermass (Fuglister 1972; Lai and Richardson[4]). These rings (as opposed to the "cold core" within the ring) are bits of the warm Gulf Stream. They are numerous, physically large, temporally persistant, and are known to carry with them large populations of organisms. Such populations may persist for months or years (Ortner et al. 1978). Other species which occur primarily in the Atlantic equatorial current system show distributions very like *H. micans*, presumably as the result of occasional captures of specimens carried by cold-core rings (Nafpaktitis et al. 1977).

Cold core rings are also produced by the Kuroshio Current (Hori 1970; Kawai 1972). When sufficient samples become available, *H. micans* will probably show a distribution in the western half of the North Pacific central watermass very

[4]Lai, D. Y., and P. L. Richardson. 1977. Distribution and movement of cyclonic Gulf Stream Rings. Tech. Rep. Ref. No. 77-1, Graduate School of Oceanography, Univ. Rhode Island, Kingston, R.I.

FIGURE 3.—*Halobates micans* distribution in the EASTROPAC area, showing number of insects caught per tow. When insects were caught in more than one tow at each station the numbers are separated by a comma. Small dots represent negative stations, large dots are positive stations.

much like that seen in the western North Atlantic. This is because the general circulation patterns of the North Atlantic and the North Pacific are similar, and the scattered records in the western midlatitudes in the North Atlantic are probably a result of the Gulf Stream.

In the eastern tropical Pacific, *H. micans* does not often occur south of lat. 10° S or north of lat. 20° N (Figure 3). The southern border of its distribution is well defined by the EASTROPAC sampling program. The northern border could be an artifact of that sampling program, since distributions of both samples and the species approximately coincide. However, many negative EASTROPAC samples were taken north of the edge of the species distribution (Figure 3), a large number of California Current samples have also been negative for the species (Cheng unpubl. data), and other sampling programs have shown the same feature (Figure 2). These combine to convince us that the northern border shown in Figure 3 is not artificial.

Halobates sobrinus seems to be confined to the equatorial upwelling regions off the west coast of Central America, with some northward extension along the Mexican coast (Figure 2). Although both the North and South Equatorial Currents could

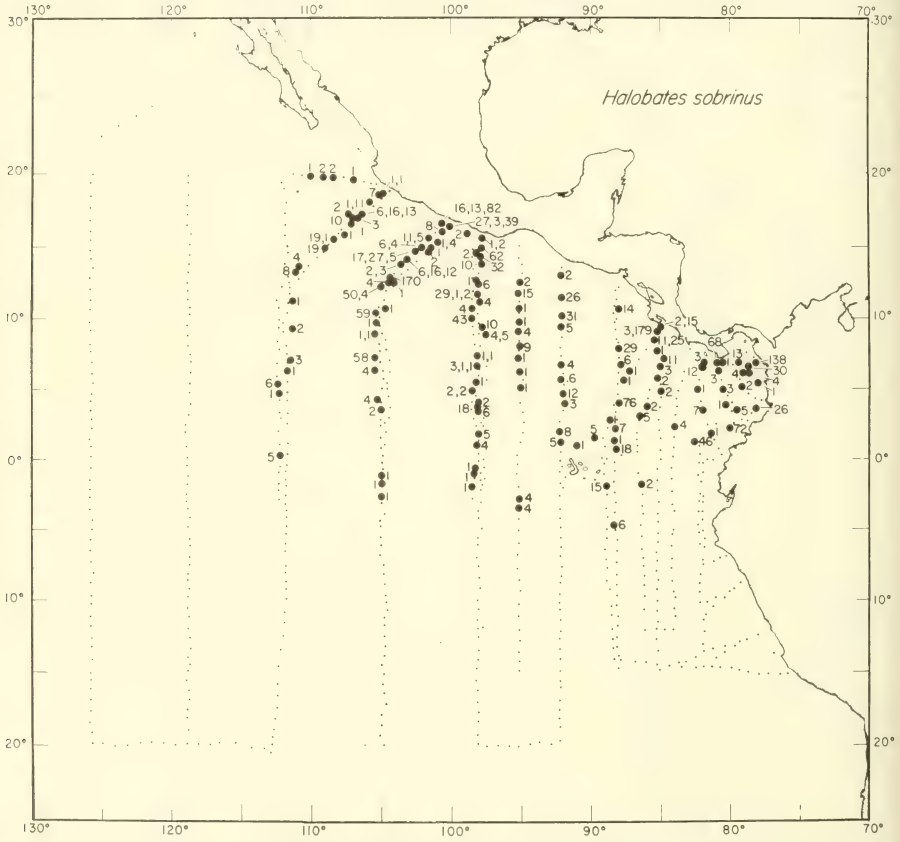


FIGURE 4.—*Halobates sobrinus* distribution, as in Figure 3.

carry the species westward (Sverdrup et al. 1942), its range shows no such effect (Figures 2, 4). More samples from the central equatorial Pacific are needed to confirm the apparent abrupt termination of the species' range at about long. 112° W. In the EASTROPAC area, *H. sobrinus* does not occur west of about long. 112° W or south of lat. 5° S (Figure 4). While the ranges of *H. sobrinus* and *H. micans* overlap somewhat, their regions of high population density (defined as samples with ≥10 individuals) overlap very little (Figure 5).

Halobates sericeus is clearly confined to the central watermasses of the North and South Pacific. The three records of this species on the Equator (at long. 82° W, 119° W, and 129° W; Figure 2) appear likely to be misidentifications (data from Herring 1961). However, present data also include one individual which lies well outside the apparent range of the species (Figure 6; at long. 100° W, lat. 16° N) and we have reconfirmed the identification of this specimen. Since these insects are usually <4 mm long, individuals may be carried long distances by the wind. This could explain such isolated captures. *Halobates sericeus* does not occur in the upwelling areas of the eastern tropical Pacific, nor in the zonal equatorial currents (Fig-

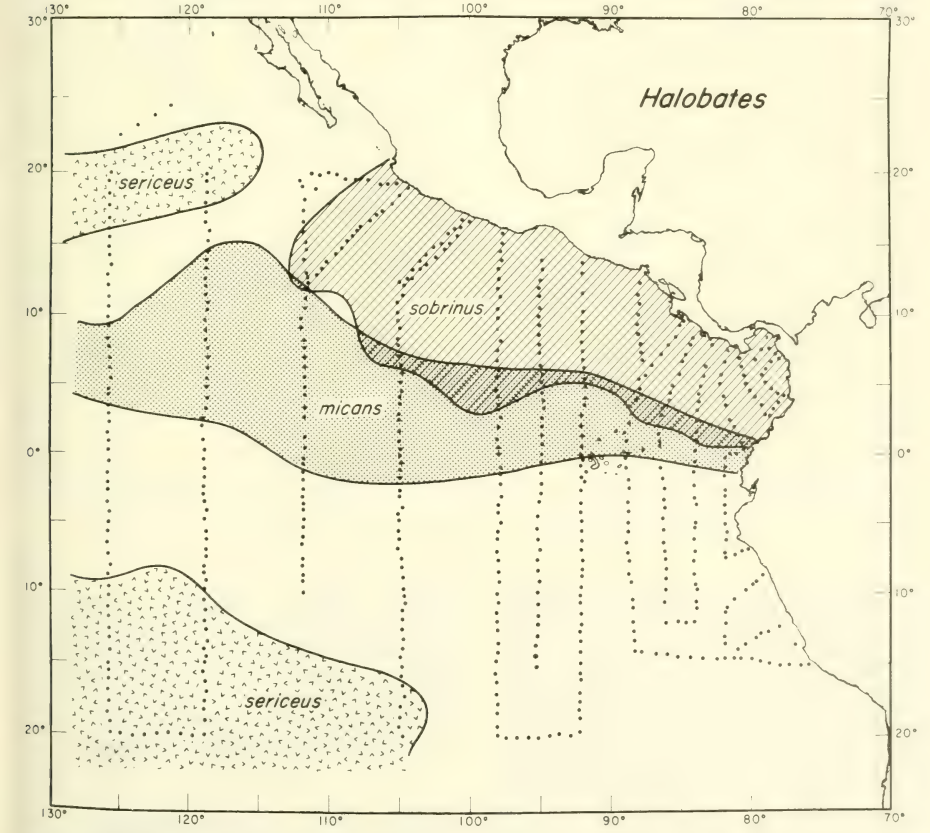


FIGURE 5.—Areas of high population densities of three *Halobates* species in the EASTROPAC area. "High" is defined as occurrence of $N \geq 10$ individuals in at least one sample (area per sampe ≈1,800 m²).

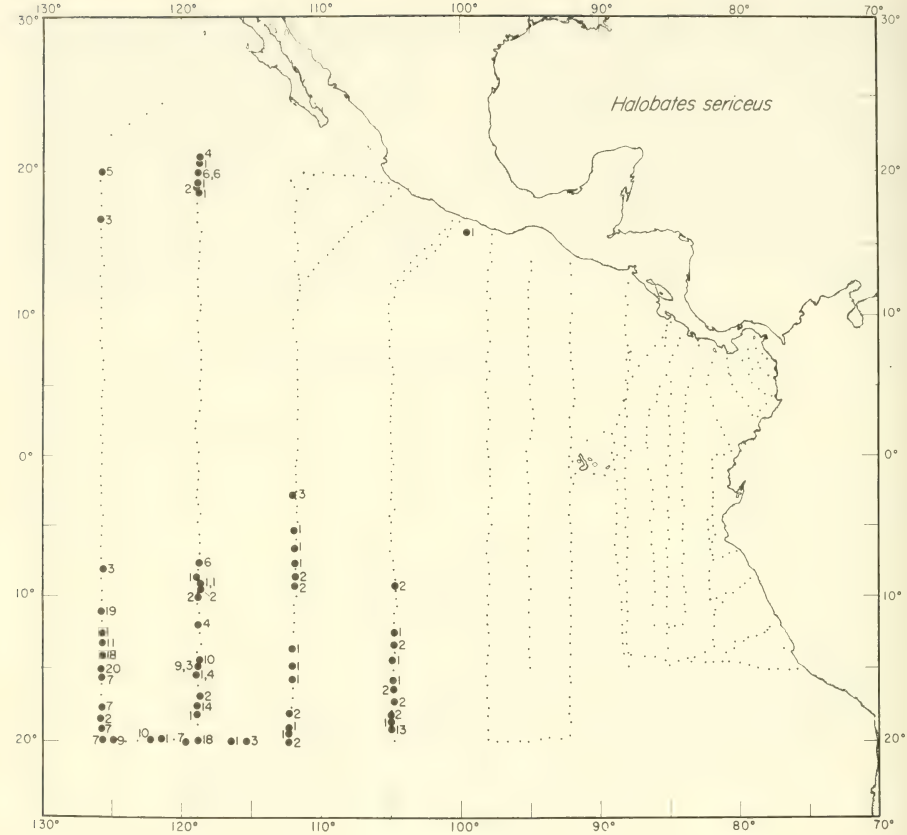


FIGURE 6.—*Halobates sericeus* distribution, as in Figure 3.

ure 6). It occurs completely outside the range of *H. sobrinus* (Figures 4, 5) and shows only very small overlap with *H. micans* (Figures 3, 5).

Halobates splendens, rarest of the four EASTROPAC species, has not been found north of about lat. 8° N (Figure 7). The captures reported in the Chile Current (Figure 2) indicate that this species may be primarily associated with the central South Pacific watermass or the South American coastal current System. Sampling in this region is insufficient at present to permit better definition of its range.

The distributions of *Halobates* spp. appear to be controlled by two major influences: 1) the patterns agree with broad, general surface-circulation patterns, and 2) species' regions of high abundance generally tend not to overlap. We do not know whether the nonoverlap is due to competitive effects or to physiological adaptations by each species to a particular environmental regime.

Abundance

Two important difficulties in deriving quantitative estimates of *Halobates* spp. abundance are: 1) most neuston nets (including ours) tend to skip out

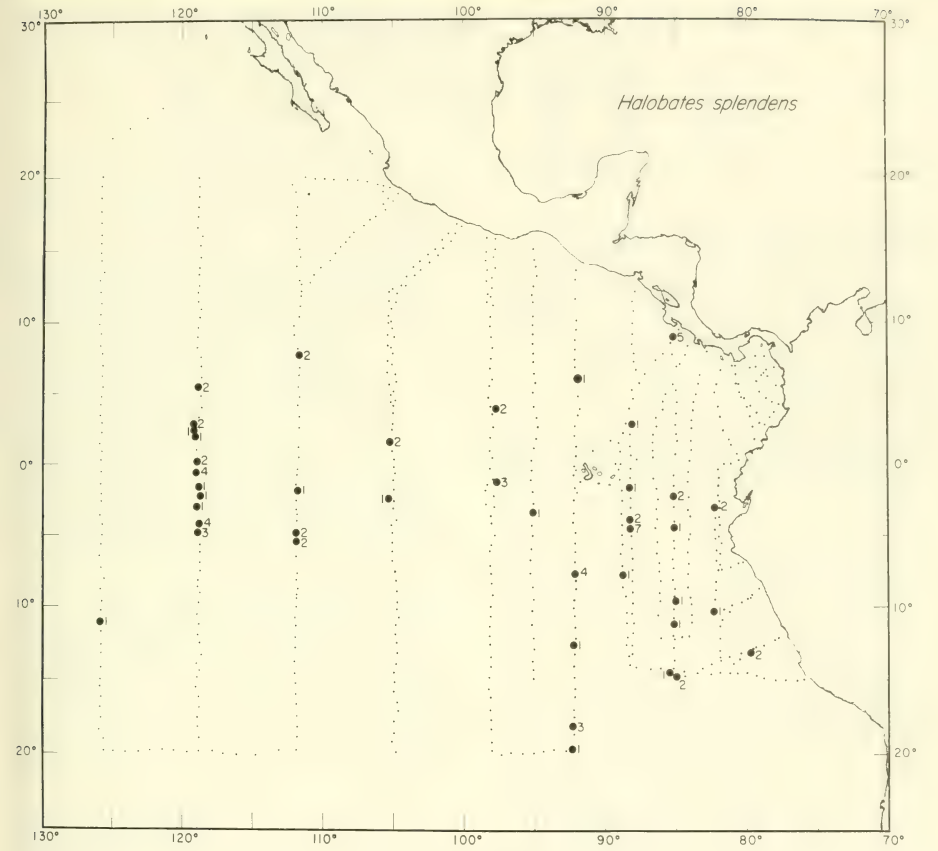


FIGURE 7.—*Halobates splendens* distribution, as in Figure 3.

of the water in anything except calm weather, making estimation of area sampled or volume filtered difficult; and 2) these insects are known to avoid nets but the extent of avoidance is unknown (Cheng 1973c; Cheng and Enright 1973). However, the samples used in this study resulted from replicate tows and may therefore be reasonably compared with one another and used to set lower limits on abundance.

Our data showed that in *H. micans*, *H. sobrinus*, and *H. splendens* numbers of adults are about twice that of nymphs (Table 2). This may be a result of several factors: 1) nymphs might avoid the net more actively than adults (unlikely); 2) nymphs are smaller than adults and may wash through the meshes of the net more easily (possible); 3) nymphs might have been missed in sorting (unlikely; samples have been rechecked); and 4) aspects of their natural history might produce such a distribution (e.g., heavy predation on nymphs plus long life-span of adults). Data do not exist to test hypotheses 1) and 4). We can offer no explanation for the differences between *H. sericeus* and the other three species.

Since *H. micans* and *H. sobrinus* accounted for almost 90% of total individuals caught (65.6 and

TABLE 2.—Numbers of *Halobates* spp. caught in the EASTROPAC area. Roman numerals = nymphal instar number.

Species	Individuals	Adults	Nymphs	Numbers per life stage					Adults	
				I	II	III	IV	V	♂	♀
H. micans	754	490	264	22	15	45	83	99	204	286
H. sobrinus	2,156	1,388	768	63	75	179	178	273	693	695
H. sericeus	285	126	159	19	20	34	31	55	55	71
H. splendens	77	50	27	0	5	6	8	8	20	30

23.3%, respectively), we will confine further discussions of abundance to these two species.

In an attempt to determine if *H. micans* and *H. sobrinus* are randomly distributed on the ocean surface, curves of "number per tow" vs. "number of tows with that number of insects" were compared with Poisson probability density functions. Such tests are appropriate for these data (Sokal and Rohlf 1969) but difficult to perform because of uncertainty as to how many "zero" catches should be included in the divisor when calculating a mean catch-per-tow. Maximum likelihood estimates of the means for truncated Poisson distributions (i.e., lacking a zero class) were therefore calculated for both species (Cohen 1960), and the frequency distributions of Figure 8 were compared with the calculated (expected) Poisson distribution. Chi-square tests of expected vs. observed were very highly significant for both species ($P<<0.001$), leading to the rejection of the null hypothesis that observed distribution cannot be told from a Poisson. We therefore conclude that both *H. micans* and *H. sobrinus* are nonrandomly distributed across the ocean surface in the regions where they occur.

The coefficient of disperson ($s^2/\bar{x}$, Sokal and Rohlf 1969) for *H. sobrinus* is ≈46.0 and for *H. micans* is ≈5.8. We thus conclude that both species are very strongly clumped ("patchy"), *H. sobrinus* more so than *H. micans*. The numbers per sample also vary widely, e.g., from 0 to 179 for *H. sobrinus*. It is not known what environmental factors cause one location to provide higher catches than another. Assuming optimum sampling conditions (perfect net performance, etc.), the highest population densities calculatable for each of the four species are presented in Table 3. These are lower limits because of probable net avoidance

TABLE 3.—Highest estimates of population density for *Halobates* spp. in the EASTROPAC area.

Species	Maximum no./sample	Maximum observed population (no./km²)
H. micans	39	2×10^3
H. sobrinus	179	1×10^4
H. sericeus	20	1×10^3
H. splendens	7	4×10^2

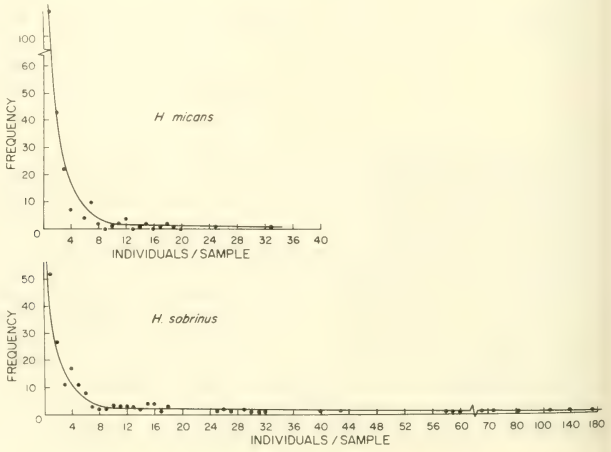


FIGURE 8.—Frequency distribution of *Halobates micans* and *H. sobrinus* in positive samples. The number of insects caught per tow is plotted against the number of tows containing that many insects. "Zero catches" are excluded (see text).

behavior (Cheng 1973c; Cheng and Enright 1973). Actual maximum densities are probably considerably higher.

Cooccurrence

The incidence of cooccurrence of two or more *Halobates* spp. in our samples was low. Out of 498 positive samples, only 33 contained two species (Table 4); 1 sample had three species. This confirms the impression given by distributional maps (Figures 2-7) that the various species seldom occur together. Separation of distribution holds, even for species with overlapping ranges (*H. micans* and *H. sobrinus*). In those samples in which these two species cooccur, there is no correlation of abundance (Figure 9). This indicates that local variations in abundance of these two species are not merely responses to vectorial (i.e., physical) forces. If vectorial forcing were the case, then the two species should be abundant in the same samples and be positively correlated when they cooccur.

The mean number of individuals per positive tow (pooled for all cruises and by cruise) is much higher in *H. sobrinus* than in *H. micans*, although the percentage of positive tows is similar for both species (Table 5). However, the highest frequency of capture (i.e., percentage of positive tows) for *H. sobrinus* occurred in the same series as the lowest frequency for *H. micans* (Figure 10). This may represent some temporal partitioning of resources, but is undoubtedly partly a function of the species' nonoverlapping centers of high abundance

TABLE 4.—Cooccurrences of *Halobates* spp. in 498 positive EASTROPAC samples (at least one specimen of each species per sample).

Species	*H. micans*	*H. sobrinus*	*H. sericeus*	*H. splendens*
H. micans	—	28	1	1
H. sobrinus		—	0	4
H. sericeus			—	1
H. splendens				—

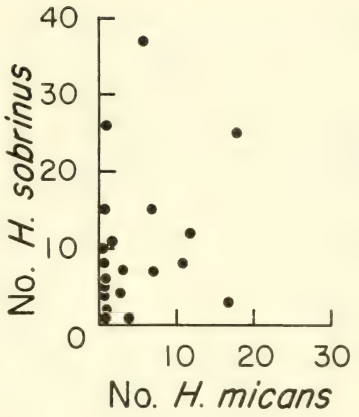


FIGURE 9.—Abundance of *Halobates micans* and *H. sobrinus* in samples in which the species cooccurred. Abundance of the two species is not correlated (Olmstead and Turkeys' corner test for associativity, $P>0.05$).

(Figure 5), differences in cruise tracks, and differences in times of the year (Figure 1).

Temperature Effects

Temperature of surface waters appears to be important in the distribution of *Halobates* spp. Figure 11 shows the number of individuals per positive sample plotted against surface water temperature for both March and August 1967. Abundance was very low in samples taken at <24° C and >28° C. The optimal temperature band appears to be quite narrow. The shape of these curves is not an artifact of the number of samples obtained at each temperature: the data have been standardized to a per tow basis and there were many tows taken at each temperature.

TABLE 5.—Occurrence of *Halobates micans* and *H. sobrinus* by EASTROPAC cruise series.

Cruise series	*H. micans*			*H. sobrinus*		
	No. positive tows	Total no. insects	Mean no. insects/tow	No. positive tows	Total no. insects	Mean no. insects/tow
10	76	387	5.1	50	568	11.4
20	23	43	1.9	28	436	15.6
30	8	10	1.3	17	65	3.8
40	17	61	3.6	30	446	14.9
50	20	45	2.3	18	192	10.7
60	22	50	2.3	5	20	4.0
70	52	196	3.8	29	382	13.2
Totals	218	792	3.6	177	2,109	11.9
Positive tows, %	13.2			10.7		

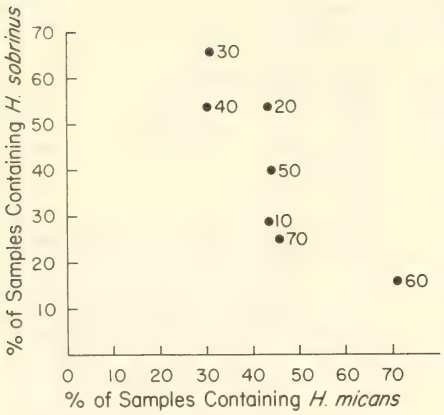


FIGURE 10.—Percentage of samples containing *Halobates micans* and *H. sobrinus* compared by cruise series (Table 1). Series numbers are shown beside each point. Note inverse relationship.

CONCLUSIONS

Four pelagic species of *Halobates*—*H. micans, H. sericeus, H. sobrinus,* and *H. splendens*—are found in the eastern tropical Pacific area. Within the EASTROPAC area, the ranges of the four species agree well with dominant oceanic zones or domains; e.g., tropical-equatorial, central watermass, and coastal upwelling. The worldwide distributions of the four species in the Pacific Ocean have also been found to agree with recognized oceanic domains (Herring 1961; Savilov 1967) although at present data are still insufficient to clearly define some boundaries, especially in the southern tropical Pacific. Although species may cooccur in the EASTROPAC area, geographical regions of high abundance for *H. micans, H. sobrinus,* and *H. sericeus* show little overlap. Our estimates for maximum abundance (lower bounds) for the two more abundant species, *H. micans* and *H. sobrinus*, are 400-10,000/km². This is likely to be conservative because they can avoid nets and because the neuston net used in our study did not sample in an ideal manner. We found *Halobates* to be most abundant in 24°-28° C waters. The two abundant species showed very patchy distributions. Present temporal and spatial coverages are insufficient to allow us to define possible seasonal variations in population density or structure.

It seems clear that the distributions of *Halobates* spp., inhabiting a strictly two-dimensional world, are governed by the same oceanic processes which shape the distributions of other marine species that inhabit a three-dimensional world.

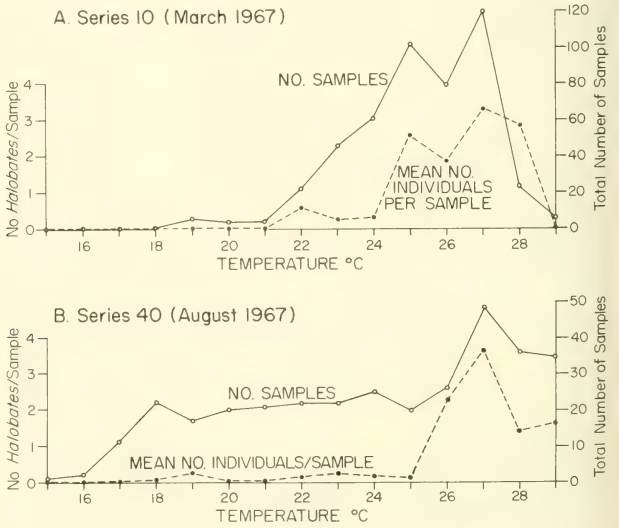


FIGURE 11.—Number of *Halobates* specimens (data for all four species combined) per positive sample vs. sea-surface temperatures. A. Series 10, March 1967. B. Series 40, August 1967. (Exact dates and area covered given in Table 1 and Figure 1.)

ACKNOWLEDGMENTS

This work was partially supported by the U.S. Office of Naval Research (Codes 461, 482, 484; contracts N00014-78-C-0697, N00014-79-C-0200, and N00014-75-C-0152) and by the National Science Foundation (grant OCE76-19786).

LITERATURE CITED

AHLSTROM, E. H.
1971. Kinds and abundance of fish larvae in the eastern tropical Pacific, based on collections made on EASTROPAC I. Fish. Bull., U.S. 69:3-77.
1972. Kinds and abundance of fish larvae in the eastern tropical Pacific on the second multivessel EASTROPAC survey, and observations on the annual cycle of larval abundance. Fish. Bull., U.S. 70:1153-1242.

ANDERSEN, N. M.
1977. Fine structure of the body hair layers and morphology of the spiracles of semiaquatic bugs (Insecta, Hemiptera, Gerromorpha) in relation to life on the water surface. Vidensk. Medd. Dan. Naturhist. Foren. 104:7-37.

ANDERSEN, N. M., AND J. T. POLHEMUS.
1976. Water-striders (Hemiptera: Gerridae, Veliidae, etc.). *In* L. Cheng (editor), Marine insects, p. 187-224. North-Holland Publishing Co., Amsterdam.

BRINTON, E.
1979. Parameters relating to the distributions of planktonic organisms, especially Euphausiids in the eastern tropical Pacific. Prog. Oceanogr. 8:125-189.

CHENG, L.
1973a. *Halobates*. Oceanogr. Mar. Biol. Annu. Rev. 11:223-235.
1973b. Marine and freshwater skaters: differences in surface fine structures. Nature (Friday) 242:132-133.
1973c. Can *Halobates* dodge nets? I: By daylight? Limnol. Oceanogr. 18:663-665.
1974. Notes on the ecology of the oceanic insect *Halobates*. Mar. Fish. Rev. 36(2):1-7.
1975a. Marine pleuston—animals at the sea-air interface. Oceanogr. Mar. Biol. Annu. Rev. 13:181-212.
1975b. Insecta Hemiptera: Heteroptera, Gerridae, Genus *Halobates*. Fiches Identif. Zooplancton 147, 4 p.

CHENG, L., M. DOECK, AND D. A. I. GORING.
1978. UV absorption by gerrid cuticles. Limnol. Oceanogr. 23:554-556.

CHENG, L., AND J. T. ENRIGHT.
1973. Can Halobates dodge nets? II. By moonlight? Limnol. Oceanogr. 18:666-669.

CHENG, L., AND C. H. FERNANDO.
1969. A taxonomic study of the Malayan Gerridae (Hemiptera: Heteroptera) with notes on biology and distribution. Orient. Insects 3:97-160.

COHEN, A. C., JR.
1960. Estimating the parameter in a conditional Poisson distribution. Biometrics 16:203-211.

FUGLISTER, F. C.
1972. Cyclonic rings formed by the Gulf Stream, 1965-66. *In* A. L. Gordon (editor), Studies in physical oceanography; a tribute to George Wüst on his 80th birthday, Vol. 1, p. 137-168. Gordon and Breach, N.Y.

HERRING, J. L.
1961. The genus *Halobates* (Hemiptera: Gerridae). Pac. Insects 3:223-305.

HORI, S.
1970. Horizontal flow in the Kuroshio Extension area. *In* K. Sugawara (editor), The Kuroshio II: Proceedings of the second symposium on the results of the cooperative study of the Kuroshio and adjacent regions, p. 61-64. Tokyo.

KAWAI, H.
1972. Hydrography of the Kuroshio Extension. *In* H. Stommel and K. Yoshida (editors), Kuroshio: Physical aspects of the Japan Current, p. 235-352. Univ. Wash. Press, Seattle.

LEE, R. F., AND L. CHENG.
1974. A comparative study of the lipids of water-striders from marine, estuarine and freshwater environments: *Halobates, Rheumatobates, Gerris* (Heteroptera: Gerridae). Limnol. Oceanogr. 19:958-965.

LOVE, C. M. (editor).
1970-75. EASTROPAC Atlases. 10 vol. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Circ. 330.

MCGOWAN, J. A.
1971. Oceanic biogeography of the Pacific. *In* B. M. Funnell and W. R. Riedel (editors), The micropaleontology of the oceans, p. 3-74. Camb. Univ. Press, Lond.
1974. The nature of oceanic ecosystems. *In* C. B. Miller (editor), The biology of the oceanic Pacific, p. 9-28. Oreg. State Univ. Press.

NAFPAKTITIS, B. G., R. H. BACKUS, J. E. CRADDOCK, R. L. HAEDRICH, B. H. ROBISON, AND C. KARNELLA.
1977. Family Myctophidae. *In* R. H. Gibbs, Jr. (editor-in-chief), Fishes of the western North Atlantic, part seven, p. 13-265. Sears Found. Mar. Res., Yale Univ. Mem. 1.

ORTNER, P. B., P. H. WIEBE, L. HAURY, AND S. BOYD.
1978. Variability in zooplankton biomass distribution in the northern Sargasso Sea: the contribution of Gulf Stream cold core rings. Fish. Bull., U.S. 76:323-334.

REID, J. L., E. BRINTON, A. FLEMINGER, E. L. VENRICK, AND J. A. MCGOWAN.
1978. Ocean circulation and marine life. *In* H. Charnock and Sir George Deacon (editors), Advances in oceanography, p. 65-130. Plenum Press, N.Y.

SAVILOV, A. I.
1967. Oceanic insects of the genus *Halobates* (Hemiptera, Gerridae) in the Pacific. Oceanology 7:252-261.

SCHELTEMA, R. S.
1968. Ocean insects. Oceanus 14(3):9-12.

SOKAL, R. R., AND F. J. ROHLF.
1969. Biometry. The principles and practice of statistics in biological research. W. H. Freeman, San Franc., 776 p.

SVERDRUP, H. U., M. W. JOHNSON, AND R. H. FLEMING.
1942. The oceans. Their physics, chemistry and general biology. Prentice Hall, N.Y., 1087 p.

TSUCHIYA, M.
1974. Variation of the surface geostrophic flow in the eastern intertropical Pacific Ocean. Fish. Bull., U.S. 72:1075-1086.

WILCOX, R. S.
1972. Communication by surface waves. Mating behavior of a water strider (Gerridae). J. Comp. Physiol. 80:255-266.

OCCURRENCE, MOVEMENTS, AND DISTRIBUTION OF BOTTLENOSE DOLPHIN, *TURSIOPS TRUNCATUS*, IN SOUTHERN TEXAS

SUSAN H. SHANE[1]

ABSTRACT

Boat and land observations of free-ranging bottlenose dolphins, *Tursiops truncatus*, near Port Aransas, Texas, provided data on seasonal occurrence, daily movements, and individual distribution patterns. Censuses revealed that the winter population in the study area was twice the size of the summer population. Individual dolphins were variously identified as summer residents, winter residents, or year-round residents in the study area. There was a significant relationship between dolphin movements and tide in some sections of the study area. Dolphins consistently moved against the ebb tide and sometimes against the flood tide in these sections. Time of day was significantly related to dolphin movements in a few sections of the study area. Part or all of the study area was included in the home ranges of several individually recognizable dolphins.

Only three long-term studies of free-ranging Atlantic bottlenose dolphins, *Tursiops truncatus*, have been conducted (Würsig and Würsig 1977, 1979; Hogan[2]; Irvine et al.[3]). Bottlenose dolphins in Texas have been studied only opportunistically by Gunter (1942, 1943, 1951). Lack of detailed information on free-ranging *T. truncatus* provided an incentive for a 1-yr study of bottlenose dolphins in southern Texas. This paper presents data on seasonal occurrence, daily movements, and individual distribution patterns of dolphins in the study area.

METHODS

The study area was located near Port Aransas, Texas, (lat. 27°50′15″ N; long. 97°02′45″ W) and included seven sections (Figure 1). Aransas Pass is the shipping outlet into the Gulf of Mexico for the Port of Corpus Christi. The next open pass through which dolphins could enter or leave the Gulf is Cedar Bayou, a natural pass, located 37 km to the northeast. Sections 1, 2, and 6 are dredged to a depth of 14 m and are all used by large tankers and a variety of other boats. Sections 3 and 7 are dredged to a depth of 5 m and are used by commercial and sport fishing boats, barges, and pleasure boats. Sections 4 and 5 average 2-3 m deep and are frequented only by small fishing boats. The entire study area covers approximately 34 km^2.

Between 1 June 1976 and 31 May 1977, I spent 1,065 h observing dolphins, either from a 4 m Boston Whaler[4] or from land. Opportunistic observations were made from June through December 1977. Uniquely marked dorsal fins (Würsig and Würsig 1977) were used to identify 21 individual dolphins, and these individuals provided information on distribution and seasonal movements.

I defined the seasons as follows: 1) summer, June-August; 2) fall, September-November; 3) winter, December-February; 4) spring, March-May. Initially, air and water temperatures from the U.S. Coast Guard Station at Port Aransas were used, but after 1 December 1976 I collected these data at the beginning of each day in a harbor off Aransas Pass. Mean air and water temperatures were 28.2° and 28.4° C for summer 1976, 18.7° and 18.8° C for fall 1976, 11.2° and 11.4° C for winter 1976-77, and 22.5° and 22.7° C for spring 1977.

Zigzag censuses, conducted an average of four times (range = 0-9) per month in each section of the study area, were used to estimate population size. A zigzag census was conducted by piloting the

[1]Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843; present address: National Fish and Wildlife Laboratory, 412 N.E. 16th Avenue, Gainesville, FL 32601.

[2]Hogan, T. 1975. Untitled draft of M.S. thesis. Unpubl. manuscr., 42 p. Univ. Rhode Island, Kingston.

[3]Irvine, A. B., M. D. Scott, R. S. Wells, J. H. Kaufmann, and W. E. Evans. 1979. A study of the activities and movements of the Atlantic bottlenosed dolphin, *Tursiops truncatus*, including an evaluation of tagging techniques. Available National Technical Information Service, 5285 Port Royal Road, Springfield, VA 22151 as PB-298 042.

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Manuscript accepted January 1980.
FISHERY BULLETIN: VOL. 78, NO. 3, 1980.

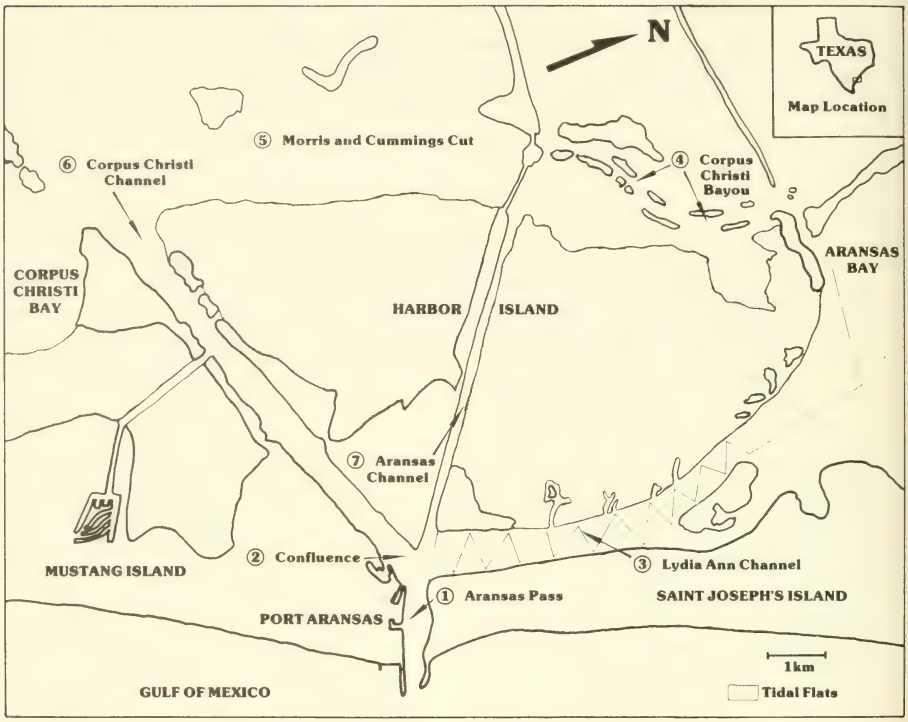


FIGURE 1.—Bottlenose dolphin study area near Port Aransas, Texas. Circled numbers designate the seven sections of the study area: 1) Aransas Pass, 2) the Confluence, 3) Lydia Ann Channel, 4) Corpus Christi Bayou, 5) Morris and Cummings Cut, 6) Corpus Christi Channel, and 7) Aransas Channel. The boundaries of the study area are the ends of the jetties at the southeast end of section 1, the mouth of Aransas Bay to the northeast, the mouth of Corpus Christi Bay to the southwest, and the islands along the northwest border of sections 4 and 5. The zigzag line drawn through section 3 shows the path followed while conducting zigzag censuses of dolphins. Similar paths were followed while censusing dolphins in the other sections.

boat at slow speed back and forth through a section and counting all dolphins sighted (Figure 1). A total of 335 zigzag censuses was conducted during 201 h during the 1-yr study. The average time per census was 23.9 min for Aransas Pass, 11.0 min for the Confluence, 55.7 min for Lydia Ann Channel, 28.3 min for Corpus Christi Bayou, 63.5 min for Morris and Cummings Cut, 52.6 min for Corpus Christi Channel, and 25.6 min for Aransas Channel.

Data on direction of dolphin movement, tidal state, and time of day were used to identify daily movement patterns. The terms used to describe direction of movement in sections 1, 3, and 6 are "up" for movement toward the bays and "down" for movement toward the Gulf of Mexico. Time of day is divided into three periods: early (0700-0900 h), midday (1000-1300 h), and late (1400-1900 h). Very few observations were made from 2000 to 0600 h, so this time period is not considered. The chi-square test was used to determine whether there was a significant relationship between dolphin movements and tide and time of day. When a relationship was found to be significant ($P<0.01$), the strength of the relationship was measured by Cramer's V (Nie et al. 1970).

RESULTS

Seasonal Occurrence

Seasonal occurrence patterns were derived from seasonal variation in dolphin numbers and from observations of individual dolphins. The monthly mean number of dolphins in the study area varied from a low of 48 in October (range = 8-104) (the September low is inaccurate because no zigzag censuses were conducted in some sections) to a high of 164 in January (range = 65-281) (Figure 2). Dolphin abundance declined from summer to fall, rose in the winter, and declined again in the spring. Boat and land observations from August through December 1977 showed the same pattern as the previous fall and early winter: dolphin numbers declined noticeably in early fall and then increased to higher than summer numbers in November and December.

Sightings of identifiable dolphins confirmed a seasonal occurrence in the study area. Sixteen of the 19 recognizable dolphins in the study area were seen on 5 or more days and were identified by the fifth month of the study. The other three dolphins were seen on <5 d or were not identified until the eighth month of the study. Three patterns of seasonal occurrence in the study area were demonstrated by the 16 dolphins (Table 1). Four individuals (Thick Fin, Jagger, Notched Fin, and Short Triangle) were predominantly spring and summer residents: over 60% of the days each was seen in the study area occurred during spring and summer and <40% occurred during fall and winter. Five individuals (Lumpy, Cloud, Bent Fin, Twin, and Tiki) were predominantly fall and winter residents: over 60% of the days each was seen in the study area occurred during fall and winter and <40% occurred during spring and summer. The remaining seven dolphins spent approximately the same amount of time in the study area during spring and summer as during fall and winter.

My observations from June through December 1977 confirmed the seasonal occurrence pattern of some dolpins established during the 1-yr study. Lumpy, a fall and winter resident who had been seen only between 20 November 1976 and 2 February 1977, was seen again on 1 and 3 December 1977. Bent Fin, a fall and winter resident who was seen regularly from October 1976 through February 1977 and then only on 3 d through November 1977, was again sighted in the study area on 5 and 8 December 1977. I saw Thick Fin (spring and summer resident) in the study area frequently from June 1977 to 8 September 1977 but never after that through December 1977, when I left the

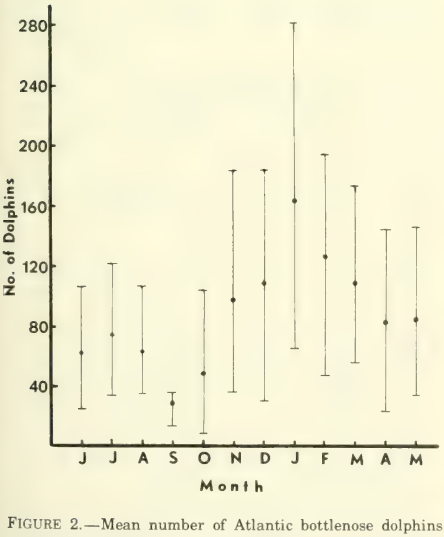


FIGURE 2.—Mean number of Atlantic bottlenose dolphins counted in the study area near Port Aransas, Texas, for each month from June 1976 through May 1977. Ranges are indicated by the vertical lines. The September count is unreliable because an insufficient number of censuses were conducted that month.

TABLE 1.—Seasonal occurrence of 16 bottlenose dolphins in the Port Aransas, Texas, area. Percentage of days each dolphin was seen during each season and each spring and summer (Sp/S) period and fall and winter (F/W) period are given. Individual dolphin occurrence patterns suggested the spring-summer and fall-winter links. Dashes indicate that the dolphin was not identified until after that season.

Dolphin	Total days sighted	Percentage of total days					
		Sp	S	F	W	Sp/S	F/W
Thick Fin	70	36	46	17	1	82	18
Jagger	5	20	60	20	0	80	20
Notched Fin	9	0	67	22	11	67	33
Short Triangle	86	31	35	29	5	66	34
Lumpy	10	0	—	30	70	0	100
Cloud	23	9	13	22	57	22	79
Bent Fin	38	5	18	24	53	23	77
Twin	13	31	—	15	54	31	69
Tiki	28	29	7	18	46	36	64
Nicky	8	25	25	0	50	50	50
Trigger	18	50	—	28	22	50	50
Chopper	46	24	24	22	30	48	52
Teaser	27	48	—	19	33	52	48
Raggedy Ann	33	33	12	12	42	45	54
V-Tip	9	44	11	33	11	55	44
Snaggle Tooth	21	33	24	24	19	57	43

area. Poff[5] reported that Thick Fin remained predominantly a spring and summer resident and Bent Fin primarily a fall and winter resident in the study area through midsummer 1979.

Daily Movements

Field observations indicated that tide and time of day influenced the movement patterns of dolphins in some sections of the study area. Most apparent was the tendency of dolphins in the lower sections of the study area (1, 3, and 6 on Figure 1) to move up against an ebb tide. The most apparent time of day effect occurred in Morris and Cummings Cut (section 5) where dolphins moved northward early in the day, all directions at midday, and southward late in the day.

The chi-square test showed that tide and direction of movement were significantly related ($P<0.0001$) in the lower section of the study area (sections 1, 3, and 6 combined) at three separate periods of the day (early, midday, late) and at all times of day combined. At all time periods most dolphins moved up during ebb tide. During flood tide most dolphins moved down, although many moved across the channel or randomly. The association between tide and direction of movement was strongest early ($V = 0.513$) and weakest at midday ($V = 0.297$) with intermediate values late ($V = 0.410$) and at all times combined ($V = 0.407$). Direction of movement and tide were significantly related in four of the six sections of the study area considered (Table 2).

The relationship between direction of movement and time of day also proved significant in four out of six sections under some conditions (Table 3). The observations on dolphin movements in Morris and Cummings Cut were quantitatively confirmed, and the association between direction of movement and time of day was stronger in that section than in any other section (see Cramer's V values in Table 3).

The frequency of sightings of groups of dolphins was calculated for all of the conditions presented in Tables 2 and 3. In all cases where the relationship between the variables was significant (chi-square $P<0.01$), the group sighting data conformed with the individual sighting data.

Individual Distribution Patterns

Sightings of each recognizable individual were confined to a specific portion of the study area rather than distributed randomly throughout the

[5]M. Poff, Research Assistant, University of Texas, Marine Science Institute, Port Aransas, TX 78373, pers. commun. July 1979. (Deceased.)

TABLE 2.—Relationship between direction of movement and tide proved significant (chi-square $P<0.01$) in four sections of the Port Aransas, Texas, study area at certain times of day. Numbers in the table represent frequency of individual dolphin sightings. Cramer's V indicates strength of the relationship between the two variables, and each V is comparable with every other V.

	Tidal stages at selected times of day							
	Early		Midday		Late		All times	
Section	Ebb	Flood	Ebb	Flood	Ebb	Flood	Ebb	Flood
Aransas Pass (1) direction:								
Up	613	54	347	56	182	83	1,165	194
Down	65	200	179	80	35	74	283	357
Across/random	126	153	92	31	27	43	245	227
Chi-square	459.06		28.53		50.73		422.07	
Cramer's V	0.616		0.191		0.338		0.413	
Corpus Christi Channel (6) direction:								
Up	513	77	205	186	296	153	1,035	416
Down	86	202	70	360	33	227	192	789
Across/random	305	226	191	348	123	228	632	802
Chi-square	291.02		119.36		203.15		642.81	
Cramer's V	0.454		0.296		0.438		0.408	
Lydia Ann Channel (3) direction:								
Up	329	57	380	93	20	21	729	171
Down	13	47	59	48	5	27	77	126
Across/random	114	58	178	44	6	25	298	127
Chi-square	115.43		33.05		11.749		154.59	
Cramer's V	0.432		0.203		0.336		0.318	
Morris and Cummings Cut (5) direction:								
North	30	28	Not		12	9	149	153
South	0	16	significant		0	99	165	250
Across/random	33	0			0	10	146	112
Chi-square	[1]47.183				[1]68.620		18.90	
Cramer's V	[1]0.664				[1]0.727		0.139	

[1]Insufficient data in a given case made the chi-square test potentially invalid.

TABLE 3.—Relationship between direction of dolphin movement and time of day was significant (chi-square $P<0.01$) in four sections of the Port Aransas, Texas, study area during a few tidal stages. Numbers in the table represent frequency of individual dolphin sightings. Cramer's V indicates the strength of the relationship between the two variables, and each V is comparable with every other V.

	Time of day at selected tidal stages								
	Ebb			Flood			All tides		
Section	Early	Midday	Late	Early	Midday	Late	Early	Midday	Late
Aransas Pass (1) direction:									
Up	613	347	182	54	56	83	740	501	390
Down	65	179	35	200	80	74	398	386	175
Across/random	126	92	27	153	31	43	385	165	148
Chi-square	116.78			73.97			62.41		
Cramer's V	0.187			0.219			0.097		
Corpus Christi Channel (6) direction:									
Up	513	205	296	77	186	153	775	567	648
Down	86	70	33	202	360	227	506	724	310
Across/random	305	191	123	226	348	228	781	763	501
Chi-square	46.74			18.029			145.71		
Cramer's V	0.113			0.067			0.114		
Lydia Ann Channel (3) direction:									
Up	329	380	20	57	93	21	494	750	72
Down	13	59	5	47	48	27	125	190	60
Across/random	114	178	6	58	44	25	260	425	90
Chi-square	[1]27.335			14.717			49.50		
Cramer's V	[1]0.111			0.132			0.100		
Morris and Cummings Cut (5) direction:									
North	30	107	12	28	116	9	330	857	54
South	0	165	0	16	135	99	85	684	537
Across/random	33	113	0	0	102	10	182	1,038	165
Chi-square	[1]69.059			104.46			737.32		
Cramer's V	[1]0.274			0.318			0.306		

[1]Insufficient data in a given case made chi-square test potentially invalid.

study area. Thick Fin and Raggedy Ann used separate but adjacent portions of the study area (Figure 3). Teaser used a portion of the study area which included most of Thick Fin's portion and all of Raggedy Ann's portion (Figure 3).

The portions of the study area used by Thick Fin and Raggedy Ann were designated Region A and Region B. Region A encompassed Aransas Pass, the Confluence, Lydia Ann Channel, and Corpus Christi Channel. Five dolphins, including Thick Fin, were sighted 80% or more of the time in this region (Table 4). Region B covered Morris and Cummings Cut, and three dolphins, including Raggedy Ann, were seen 88% or more of the time there (Table 4). These three Region B dolphins consistently traveled in a large group of usually 20 or more dolphins which moved into and out of the study area through Corpus Christi Bay. Two dolphins, Teaser and Cloud, were observed often in both Regions A and B, and their sightings covered 20 km^2 and 25 km^2.

In addition to the 19 identifiable dolphins in the study area, two recognizable individuals, Southpaw and Half Fin, were sighted only in the Gulf of Mexico. Other dolphins with unique dorsal fins were seen in the gulf whenever observations were made there. These *T. truncatus* from the Gulf of Mexico were sometimes seen within meters of Aransas Pass, but they entered the study area only rarely and briefly.

As discussed earlier, many dolphins inhabited the study area on a seasonal basis. Observations of some individuals indicated their possible locations when they left the study area. On 22 February 1977 I saw Short Triangle traveling up Aransas Pass toward the bays at 11:07 a.m. and traveling down the Pass to the Gulf at 12:35 p.m. Although I made continuous observations for the remainder of the day from the shoreline of the Pass, I did not resight Short Triangle. On 18 October 1976 I saw Thick Fin entering the Gulf of Mexico; after that and until mid-March 1977, I saw Thick Fin only on 18 November 1976 and 25 January 1977. On 29 June 1979, Gruber[6] sighted Thick Fin 50 m off the Port O'Connor, Texas, jetties in the Gulf of Mexico, 100 km northeast of Port Aransas. I was able to confirm the sighting from photographs taken by Gruber. Port Aransas ferry operators, familiar with Thick Fin, reported to Gruber that they had seen Thick Fin on 24 June and again on 22 July. Bent Fin entered and left the study area through

[6]J. Gruber, graduate student, Department of Wildlife and Fishery Sciences, Texas A&M University, College Station, TX 77843, pers. commun. July 1979.

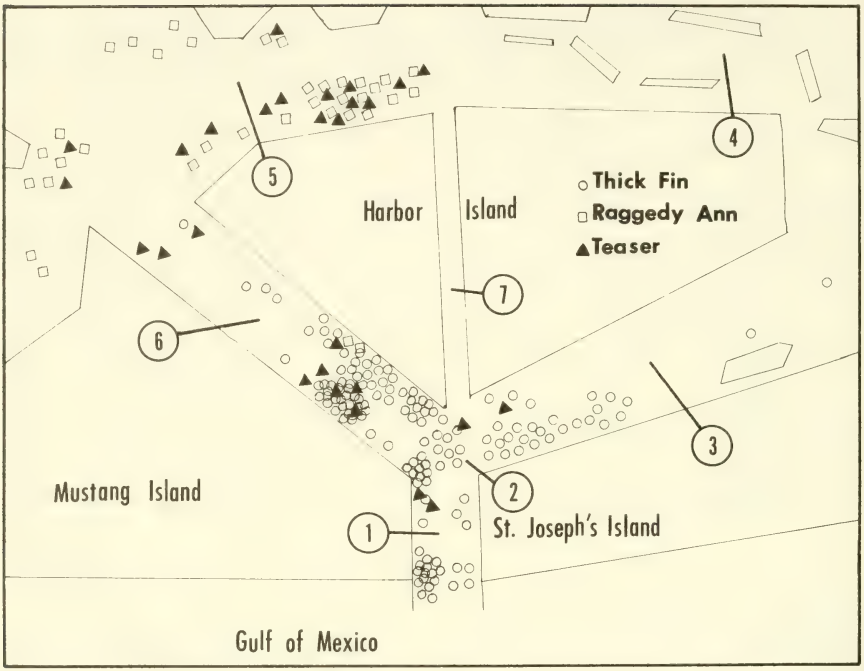


FIGURE 3.—Distribution of sightings of three bottlenose dolphins (Thick Fin, Raggedy Ann, and Teaser) near Port Aransas, Texas, during 1976-77. The map is a diagram (not drawn to scale) of the study area shown in Figure 1, and the circled numbers identify the same seven sections of the study area given in Figure 1.

TABLE 4.—Sightings of individual bottlenose dolphins in inshore waters near Port Aransas, Texas. Only dolphins sighted 25 or more times from June 1976 through May 1977 are included. Region A includes Aransas Pass (1), the Confluence (2), Lydia Ann Channel (3), and Corpus Christi Channel (6) (total area, 11 km²). Region B includes Morris and Cummings Cut (5) (total area, 14 km²).

Individual (total no. sightings)	No. sightings in Region A (%)	No. sightings in Region B (%)	No. sightings outside Regions A and B
Thick Fin (140)	140 (100%)	0	0
Short Triangle (142)	139 (98%)	0	3 (2%)
Snaggle Tooth (28)	26 (93%)	1 (4%)	1 (4%)
Bent Fin (64)	57 (89%)	3 (5%)	4 (6%)
Trigger (25)	20 (80%)	1 (4%)	4 (16%)
Raggedy Ann (36)	2 (6%)	32 (89%)	2 (6%)
Tiki (33)	4 (12%)	29 (88%)	0
Chopper (52)	3 (6%)	47 (90%)	2 (4%)
Teaser (28)	13 (46%)	15 (54%)	0
Cloud (33)	21 (64%)	8 (24%)	4 (12%)

the northeast boundary where Lydia Ann Channel joins Aransas Bay.

DISCUSSION

Seasonal Occurrence

Contrary to Gunter (1942), the present study provides evidence for seasonal variation in abundance of *T. truncatus* in Texas. As Figure 2 shows, the winter population in the study area was about twice the size of the summer population. The population increased or declined during the fall and spring as dolphins moved into or out of the study area. Irvine et al. (footnote 3) noted fewer dolphins in their study area in central west Florida during the winter than during the summer. They also observed seasonal changes in the distribution of bottlenose dolphins in that area. Seasonal migrations have been hypothesized for *T. truncatus* on the Atlantic coast (True 1890), and Caldwell and Caldwell (1972) noted variations in abundance of

T. truncatus in northeastern Florida on a seasonal basis. Würsig (1978) found no evidence for a seasonal migration of *T. truncatus* in Argentina.

The belief that the seasonal variation in abundance of bottlenose dolphins in the study area was an annual occurrence and not a result of the unusually cold winter of 1976-77 was supported by my 1977 fall and winter observations. Later observations on the seasonal presence of Thick Fin and Bent Fin in the study area by Poff (footnote 5) further substantiated the first year's data.

Bottlenose dolphins in the Port Aransas area responded to seasonal changes by emigrating out of the study area for the winter, immigrating into the study area for the winter or by remaining year-round residents. Hogan (footnote 2) and True (1890) reported the first and third patterns for *T. truncatus* in the Atlantic.

The three responses to seasonal changes exhibited by dolphins in the study area prohibit a simple explanation of seasonal occurrence patterns. Two factors cited as affecting cetacean distribution are water temperature (Gaskin 1968) and food availability (Mercer 1975). Water temperature in the study area changed from a winter mean of 11.4° C to a summer mean of 28.4° C, and this change could have had a direct or indirect effect upon dolphin movements. Food is available to dolphins both in the study area and in the Gulf of Mexico during the winter: most fish species emigrate from the bays to the Gulf for the winter, but a few species spend the winter in the bays (Gunter 1945). Three of the latter species—striped mullet, *Mugil cephalus*; sand trout, *Cynoscion arenarius*; and black drum, *Pogonias cromis*—have been found in the stomachs of bottlenose dolphins (Gunter 1942). Other fish species wintering in the bays near Port Aransas were killed by cold spells during the winters of 1940 and 1951 (Gunter 1941; Gunter and Hildebrand 1951). Of these, spot, *Leiostomus xanthurus*; croaker, *Micropogon undulatus*; sheepshead, *Archosargus probatocephalus*; spotted trout, *C. nebulosus*; pinfish, *Lagodon rhomboides*; and ribbonfish, *Trichiurus lepturus*, are eaten by *T. truncatus* (Gunter 1942; Kemp[7]). If water temperature and food availability influence the seasonal occurrence of dolphins in the study area, individual dolphins or social groups may have different temperature or food preferences.

Daily Movements

Dolphins generally move against the tide in the lower sections of the study area, although they moved against the ebb tide more consistently than they moved against the flood tide (Table 2). In all other studies where cetacean movements and tides were correlated, cetaceans moved with tidal currents (Irvine and Wells 1972; Norris et al. 1977; Irvine et al. footnote 3; Würsig[8]). Tide was significantly related to dolphin movements in only one case in the upper section of the study area, and the strength of the relationship there was weak ($V = 0.139$). In two other cases where tide and direction were significantly related in the upper section of the study area, insufficient data made the chi-square results potentially invalid. This lack of tidal effect for the upper bays agrees with the observation that gray whales moved with tidal currents in channels but ignored tidal flow in bays (Norris et al. 1977).

Dolphins consistently moved against the ebb tide in Aransas Pass where the strongest ebb tides were slightly stronger (2.5 km/h) than the strongest flood tides (2.4 km/h) (Smith 1979) and where there was a net outflow averaging 0.3 km/h (Smith 1978). Dolphins showed little or no consistency in their tide-related movements in Morris and Cummings Cut where inflow and outflow should be approximately equal in strength and net effect (Smith 1978). The tidal data indicate that dolphins respond to the dominant tidal currents in this area by moving against them, and that their movements are less affected by tide in areas where tidal effects are diluted such as in the upper bays.

Two explanations for the movement of dolphins against tidal flow seem possible. First, the countercurrent movement may represent a method of feeding. Dolphins may catch fish more easily when the fish are swimming with or being carried by the current. The possible increase in feeding efficiency might outweigh the energy expenditure required to move against a strong current. There is evidence that more fish move through Aransas Pass during ebb tides than during flood tides: "The difference in catch [of fishes in Aransas Pass] between flood tide collections and ebb tide collections was tremendous. Few specimens were collected during flood tide, although the tide trap was low-

[7]Kemp, R. J. 1949. Report on stomach analysis-Delphininae. Annual Report of the Marine Laboratory of the Texas Game, Fish and Oyster Commission for the fiscal year 1948-1949. Unpubl. manuscr., p. 111-112, 126-127.

[8]Würsig, B. 1976. Radio tracking of dusky porpoises (*Lagenorhynchus obscurus*) in the south Atlantic, a preliminary analysis. *In* FAO-ACMRR Scientific Consultation on Marine Mammals, Bergen, Norway, p. 1-21.

ered for almost as many flood tide collections as ebb tide." (Copeland 1965). Thus, dolphins may have developed a special technique for taking advantage of the concentration of food which apparently occurs in Aransas Pass during ebb tide. A second possibility is that dolphins which maintain a stationary position against a strong tidal current, as dolphins were frequently observed to do, were resting. Resting captive dolphins reportedly face against the current in the tank and use slow beats of the fluke to maintain position (McBride and Hebb 1948).

The relationship between time of day and dolphin movements was stronger in Morris and Cummings Cut than in the lower sections of the study area (Table 3). The observation that most dolphins moved northward early, all directions at midday, and southward late in the day was substantiated statistically (Table 3). The higher Cramer's V values for the time of day-direction relationship as compared with the tide-direction relationship indicated that time of day influenced direction of movement more than tide did in Morris and Cummings Cut.

The agreement between individual and group movement data in the present study showed that group size was not a significant variable. In contrast, Irvine et al. (footnote 3) found that more dolphins moved with the tide than against it, because group sizes were larger for dolphins moving with the current. They found approximately the same number of groups moving against the tide as with it.

In summary, dolphin movements were significantly related to tide and time of day in some sections of the study area. The relationship with tide was strongest in Aransas Pass where tidal effects were most pronounced and resulted in a net outflow. The relationship with time was strongest in Morris and Cummings Cut where tidal effects were diluted.

Individual Distribution Patterns

The concentration of sightings of individual dolphins in portions of the study area (Figure 3, Table 4) indicated that some individuals included parts of the study area in their home ranges (as defined by Burt 1943). Caldwell (1955) provided the first evidence for *T. truncatus* having a home range. Later, Caldwell and Caldwell (1972) proposed a dumbbell-shaped home range for *T. truncatus* which included two home ranges connected by a traveling range. At least two interpretations of my data are possible: each dolphin had one home range that extended outside of the study area, and some dolphins used different portions of their home ranges on a seasonal basis; or each dolphin had two or more home ranges connected by traveling ranges, and one home range partially or completely coincided with the study area and was used seasonally. Irvine and Wells (1972) and Saayman et al. (1973) indicated that the bottlenose dolphins which they studied exhibited localized movements, but did not specify home ranges. Wells et al. (in press) defined a home range of 85 km^2 for the dolphin herd which they studied, and they stated that it was inhabited year-round by at least some of the dolphins.

Eight of the 10 dolphins whose distributions were considered in Table 4 apparently recognized a boundary between Regions A and B. The boundary might have been a physical feature (e.g., deep channels versus large, shallow bays), or it might have been a social barrier separating social groups. Two dolphins, Teaser and Cloud, passed over the apparent boundary between Regions A and B on a regular basis. Segregation according to sex in the two regions is unlikely because Short Triangle, Raggedy Ann, and Teaser were females and used Region A, Region B, and Regions A and B, respectively.

Southpaw and Half Fin and the other dolphins with unique dorsal fins that were observed only in the Gulf of Mexico may be part of a population of *T. truncatus* that is socially or otherwise segregated from inshore *T. truncatus*. The existence of offshore *T. truncatus* has been discussed (Mitchell 1975; Odell et al.[9]). However, it is not known whether offshore and inshore *T. truncatus* are reproductively isolated and, if they are, why this is so.

The February 1977 sightings of Short Triangle and the October 1976 sighting of Thick Fin indicated that they may have spent the winter in the Gulf of Mexico or in other bay systems reached by traveling through the gulf. The June and July 1979 sightings of Thick Fin at Port Aransas and Port O'Connor showed that *T. truncatus* does move long distances in fairly short periods of time. Würsig and Würsig (1977) documented a round-trip movement of 600 km for *T. truncatus*, but this

[9]Odell, D. K., D. B. Siniff, and G. H. Waring (editors). 1975. Final report: *Tursiops truncatus* assessment workshop. Rosenstiel School of Marine and Atmospheric Sciences, University of Miami, Miami, Fla., 141 p.

movement occurred over a 15-mo period. The observations of Bent Fin entering and leaving the study area indicated that he may have inhabited the bays north of the study area during the spring and summer.

ACKNOWLEDGMENTS

I am grateful to Pat Parker and Oswald Roels of the University of Texas, Marine Science Institute, Port Aransas Marine Laboratory, for providing the research boat, gas, oil, and maintenance. Direct financial support was received from the Marine Mammal Commission, the Rob and Bessie Welder Wildlife Foundation, and the Graduate College of Texas A&M University. Thanks go to Blair Irvine, Bernd Würsig, Michael Scott, Galen Rathbun, David Schmidly, and an anonymous *Fishery Bulletin* reviewer for exhaustively critiquing several versions of the manuscript. Howard Kochman provided invaluable assistance with the statistical and computer analyses.

LITERATURE CITED

BURT, W. H.
1943. Territoriality and home range concepts as applied to mammals. J. Mammal. 24:346-352.

CALDWELL, D. K.
1955. Evidence of home range of an Atlantic bottlenose dolphin. J. Mammal. 36:304-305.

CALDWELL, D. K., AND M. C. CALDWELL.
1972. The world of the bottlenosed dolphin. J. B. Lippincott Co., Phila., 157 p.

COPELAND, B. J.
1965. Fauna of the Aransas Pass Inlet, Texas. I. Emigration as shown by tide trap collections. Publ. Inst. Mar. Sci. Univ. Tex. 10:9-21.

GASKIN, D. E.
1968. Distribution of Delphinidae (Cetacea) in relation to sea surface temperatures off eastern and southern New Zealand. N.Z. J. Mar. Freshwater Res. 2:527-534.

GUNTER, G.
1941. Death of fishes due to cold on the Texas coast, January, 1940. Ecology 22:203-208.
1942. Contributions to the natural history of the bottlenose dolphin, *Tursiops truncatus* (Montague), on the Texas coast, with particular reference to food habits. J. Mammal. 23:267-276.
1943. Letter to the editor. J. Mammal. 24:521.
1945. Studies on marine fishes of Texas. Publ. Inst. Mar. Sci. Univ. Tex. 1:1-190.
1951. Consumption of shrimp by the bottle-nosed dolphin. J. Mammal. 32:465-466.

GUNTER, G., AND H. H. HILDEBRAND.
1951. Destruction of fishes and other organisms on the South Texas coast by the cold wave of January 28-February 3, 1951. Ecology 32:731-736.

IRVINE, B., AND R. S. WELLS.
1972. Results of attempts to tag Atlantic bottlenosed dolphins (*Tursiops truncatus*). Cetology 13:1-5.

MCBRIDE, A. F., AND D. O. HEBB.
1948. Behavior of the captive bottle-nose dolphin, *Tursiops truncatus*. J. Comp. Physiol. Psychol. 41:111-123.

MERCER, M. C.
1975. Modified Leslie-DeLury population models of the long-finned pilot whale (*Globicephala melaena*) and annual production of the short-finned squid (*Illex illecebrosus*) based upon their interaction at Newfoundland. J. Fish. Res. Board Can. 32:1145-1154.

MITCHELL, E. (editor)
1975. Review of biology and fisheries for smaller cetaceans. Report and papers from a meeting of the Subcommittee on Smaller Cetaceans, International Whaling Commission, in Montreal, April 1-11, 1974. J. Fish. Res. Board Can. 32:889-983.

NIE, N. H., C. H. HULL, J. G. JENKINS, K. STEINBRENNER, AND D. H. BENT.
1970. Statistical package for the social sciences. McGraw-Hill, N.Y., 675 p.

NORRIS, K. S., R. M. GOODMAN, B. VILLA-RAMIREZ, AND L. HOBBS.
1977. Behavior of California gray whale, *Eschrichtius robustus*, in southern Baja California, Mexico. Fish. Bull., U.S. 75:159-172.

SAAYMAN, G. S., C. K. TAYLER, AND D. BOWER.
1973. Diurnal activity cycles in captive and free-ranging Indian Ocean bottlenose dolphins (*Tursiops aduncus* Ehrenburg). Behaviour 44:212-233.

SMITH, N. P.
1978. Long-period, estuarine-shelf exchanges in response to meteorological forcing. *In* J. C. J. Nihoul (editor), Hydrodynamics of estuaries and fjords, p. 147-159. Proceedings of the 9th International Liege Colloquium on Ocean Hydrodynamics, (Elsevier Oceanogr. Ser. 23). Elsevier Sci. Publ. Co., Amsterdam.
1979. Tidal dynamics of low-frequency exchanges in the Aransas Pass, Texas. Estuaries 2:218-227.

TRUE, F. W.
1890. Observations on the life history of the bottlenose porpoise. Proc. U.S. Natl. Mus. 13:197-203.

WELLS, R. S., A. B. IRVINE, AND M. D. SCOTT.
In press. The social ecology of inshore odontocetes. *In* L. M. Herman (editor), The behavior of dolphins. Wiley-Interscience, N.Y.

WÜRSIG, B.
1978. Occurrence and group organization of Atlantic bottlenose porpoises (*Tursiops truncatus*) in an Argentine Bay. Biol. Bull. (Woods Hole) 154:348-359.

WÜRSIG, B., AND M. WÜRSIG.
1977. The photographic determination of group size, composition, and stability of coastal porpoises (*Tursiops truncatus*). Science (Wash., D.C.) 198:755-756.
1979. Behavior and ecology of the bottlenose dolphin, *Tursiops truncatus*, in the South Atlantic. Fish. Bull., U.S. 77:399-412.

REPRODUCTION OF NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, OFF OREGON AND WASHINGTON

JOANNE LYCZKOWSKI LAROCHE AND SALLY L. RICHARDSON[1]

ABSTRACT

Mean relative fecundity of 21 anchovies from the northern subpopulation off Oregon and Washington was 826±49 oocytes per g ovary-free body weight, or 720±40 oocytes per g total body weight. These estimates are higher than those for the central subpopulation and may represent a racial difference between the two subpopulations. Sexual maturity is not reached in most anchovies off Oregon and Washington until the third summer (age II). The smallest anchovies found in spawning condition were 104 mm (male) and 107 mm (female) standard length. Overall male and female ratio of anchovies before and after spawning was about 1:1, but males outnumbered females 2.6:1 in regions of active spawning. Degeneration and apparent reduced growth among yolked oocytes prior to and after release of one batch of oocytes may limit the number of anchovy spawnings per season off Oregon and Washington.

Ovarian maturation is described from direct observations of whole oocytes including both normally developing and degenerating oocytes and from oocyte size-frequency distributions.

Sexually mature and immature anchovies off Oregon and Washington are segregated during the summer spawning season with mature fish occurring offshore beyond the continental shelf and immature fish occurring in nearshore coastal waters, bays, and estuaries. In winter and spring anchovies of all sizes occur together in nearshore coastal waters.

The northern anchovy, *Engraulis mordax* Girard, occurs along the west coast of North America from Cape San Lucas, Baja California, to the Queen Charlotte Islands, British Columbia (Miller and Lea 1972; Hart 1973). Within this range three subpopulations (northern, central, and southern) have been defined based on meristic characters (McHugh 1951) and blood serum proteins (Vrooman and Paloma[2]). The central subpopulation, inhabiting the general region between San Francisco, Calif., and Punta Baja, Calif., currently supports major fisheries and has been extensively studied (see most recent review, Huppert et al.[3]). The northern subpopulation, inhabiting the region north of San Francisco to British Columbia, supports only minor seasonal bait fisheries (Huppert et al. footnote 3) and has been little studied (Richardson in press).

In 1975 we initiated a study to assess the size of the stock of *E. mordax* occurring off Oregon and Washington by egg and larva survey. Knowledge of individual fecundity (the number of eggs matured as a group and spawned at one time) is essential for this method of stock assessment. Three previous estimates of northern anchovy fecundity, one for the northern subpopulation off British Columbia (Pike 1951) and two for the central subpopulation (MacGregor 1968; Hunter and Goldberg 1980) differed widely in methods and results. Pike's estimate of fecundity based on counts of all oocytes >0.20 mm was 1,369 oocytes/g total body weight. MacGregor's estimate based on counts of only the most advanced, nonhydrated, yolked oocytes (≥0.50 mm) was 574 oocytes/total body weight, and Hunter and Goldberg's estimate based on counts of ripe, hydrated oocytes was 389/g ovary-free body weight.

This study was prompted by the discrepancy between estimates of northern anchovy fecundity in the northern and central subpopulations and the general lack of information on other aspects of northern anchovy reproduction off the Oregon-Washington coast. Our primary objective was to determine anchovy fecundity in the northern subpopulation. Additional objectives were to examine length and age at sexual maturity, sex ratio, spawning frequency, ovarian maturation, seasonal gonadal condition, and patterns in geographic distribution related to the reproductive cycle.

[1]School of Oceanography, Oregon State University, Corvallis, Oreg.; present address: Gulf Coast Research Laboratory, East Beach Drive, Ocean Springs, MS 39564.

[2]Vrooman, A. M., and P. A. Paloma. 1975. Subpopulations of northern anchovy, *Engraulis mordax mordax*. Southwest Fish. Cent., NMFS, NOAA, Adm. Rep. LJ-75-62, 10 p.

[3]Huppert, D., H. Frey, A. MacCall, G. Stauffer, and O. Mathisen. 1977. First draft—Anchovy fishery management plan. 119 p. + append. Pacific Fishery Management Council, 526 S.W. Mill St., Portland, OR 97201.

Manuscript accepted January 1980.
FISHERY BULLETIN: VOL. 78, NO. 3, 1980.

METHODS

All collections of juvenile and adult northern anchovies used in this study were made off the Oregon-Washington coast, 1975-77 (Table 1, Figure 1). Because no commercial anchovy fishery exists in this region our sampling for northern anchovies was exploratory in nature and restricted by available vessel and gear facilities, most of which were not specifically designed for efficient capture of pelagic schooling fishes. In the field, fish were either frozen in plastic bags or preserved in 10% Formalin.[4] In the laboratory, frozen fish (≈1,400) were thawed, blotted on paper towels to remove excess moisture, measured (to nearest millimeter standard length, SL), and weighed (to nearest 0.1 g). Fish were slit open and sex and stage of gonadal development were recorded. Both otoliths were removed and placed in a scale envelope for later age determination. Preserved fish (≈700) were soaked in freshwater, blotted on paper towels, measured, and weighed. The paired gonads were then removed and stored in 5% Formalin. These were later weighed (wet weight) to the nearest 0.1 mg on a Mettler electronic balance.

General gonadal condition was determined using the criteria of Lagler (1956). Northern anchovies taken in March, May, and October before and after the spawning season were classified as immature or mature, depending on whether eggs or milt were grossly apparent. Fish taken in July during the spawning season were classified as either immature (no eggs or milt grossly visible), ripe (gonads firm, eggs and milt distinctly visible), or spent (gonads flaccid, often dark in color). Spent female anchovies were further characterized by the absence of oocytes in the posteriormost region of each ovary. No attempt was made to distinguish the spent condition in males or stages of recovery after spawning in either sex. A gonadal index (GI)

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Collection data for juvenile and adult northern anchovies, *Engraulis mordax*, off Oregon and Washington, 1975-77. (Gear abbreviations: ST—shrimp trawl, MST—modified shrimp trawl, IKMT—Isaacs-Kidd midwater trawl, OT—otter trawl, MOT—modified otter trawl, MCPT—modified Cobb pelagic trawl.)

Date	Gear	Sampling effort		Sampling location	Results
		No. tows	Tow duration (min)		
28 April 1975	10 m MOT	2	14	Columbia River mouth just inside north jetty and near buoy 1	0 anchovies
13 May	5 & 8 m ST	8	5	Off Columbia River mouth, buoys 1 and 2	≈500 anchovies, 95% juveniles, <100 mm SL
25-29 May	1.8 m IKMT 7 m OT	32	5-40	Off Columbia River mouth, lightship to North Head, between lat. 46°22′ and 46°10′ N and long. 124°22′ and 124° 09′ W, 20-91 m	Thousands of anchovies, 50-170 mm SL, most captured in OT on or near bottom in daytime at lat. 46° 16.6′ N, long. 124°10.9′ W, 33-35 m
30 May	5 & 8 m ST	8	5	Off Columbia River mouth, buoys 1 and 2	≈200 anchovies, mostly juveniles, 52-123 mm SL
21-25 July	1.8 m IKMT 7 m OT	53	10-20	Off Columbia River mouth, lightship to North Head, inside 91 m contour	≈700 anchovies, mostly juveniles, 70-90 mm SL, in small schools near surface at night (few mature fish and none in spawning condition)
15 Aug.	5 m ST Gill net	8 2 sets	5 ≈30	Columbia River mouth, just inside south jetty and off Gearhart, Oreg. (3.7 km south of mouth)	2 anchovies, <100 mm SL
3-8 Oct.	1.8 m IKMT 7 m OT	72	10-15	Columbia River mouth, inside river along north shore to Tongue Pt. (3.7 km from mouth) and offshore between lightship and North Head inside 91 m contour	Thousands of anchovies, only juveniles (60-90 mm SL) in river near surface, both juveniles and small adults (102-126 mm SL) offshore near bottom and in midwater
7-16 Mar. 1976	12.5 m MST	52	30	Columbia River to Coos Bay, Oreg. ≈91-183 m, on commercial shrimp grounds	Thousands of anchovies, ≈70-140 mm SL—most abundant between Astoria Canyon and Tillamook Bay
25-27 May	1.8 m IKMT 7 m OT	53	10-15	Off Columbia River mouth, 20-91 m	Thousands of anchovies, ≈50-170 mm SL, most in midwater, greatest catches in 24-27 m
9-11 July	Dipnet	—	—	≈120-140 km off Newport, Oreg.	31 adult anchovies, 104-134 mm SL, most in spawning condition (only caught at night)
19-22 July	1.8 m IKMT	36	10-20	Between Columbia River and Tillamook Bay, 120-157 km offshore	14 adult anchovies, 108-134 mm SL, most in spawning condition, small schools of fish observed near surface around ship
18-26 July 1977	40 m MCPT	11	30	Off Oregon-Washington coast between lat. 47° and 43° N and long. 124°38′ and 126° 32.8′ W from≈ 18.5 to 175+ km offshore, trawl depth usually 15-20 m	≈640 adult anchovies, 105-147 mm SL, many in spawning condition, taken only at four stations north of lat. 45°41′ N between 65 and 120 km offshore

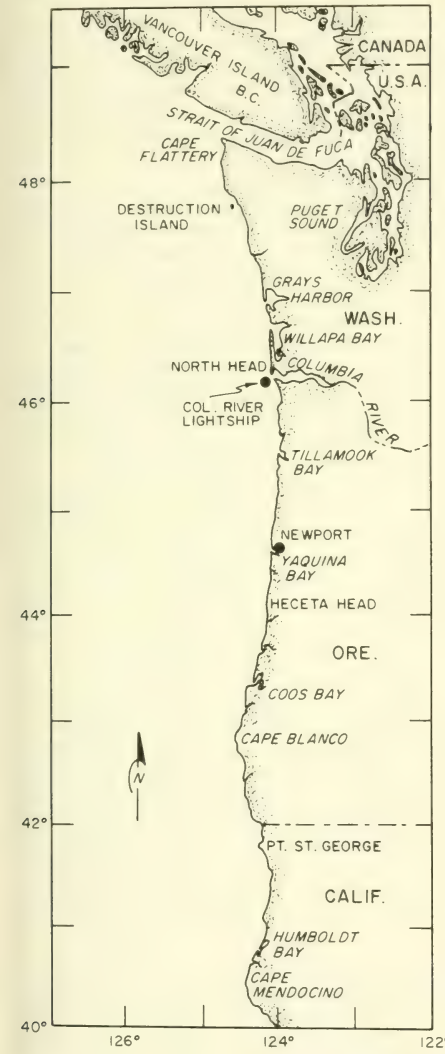


FIGURE 1.—General region of the northeastern Pacific where *Engraulis mordax* from the northern subpopulation have been collected.

was calculated for preserved fish by dividing total gonad weight by body weight (before gonad removal) and multiplying the resultant value by 100.

Oocytes from preserved ovaries were measured to the nearest 0.02 mm at 50× magnification with an ocular micrometer in a dissecting microscope. Oocyte diameter was measured until oocytes became elliptical in shape, then length (longest dimension) was measured. Measurements were made of approximately 200 oocytes/maturing fish (with oocytes $\geq$0.14 mm) and 100 oocytes/immature fish (with oocytes $\leq$0.14 mm). Fish were then grouped into 10 stages of ovarian development, depending on the modal length of the largest and most advanced group of oocytes in the ovary (Clark 1934) (Table 2). The size intervals used to define these ovarian stages were arbitrarily chosen and do not necessarily represent actual physiological stages of maturation. Composite oocyte size-frequency distributions based on all anchovies in each stage of ovarian development were derived from the mean number of oocytes in each 0.02 mm size class.

TABLE 2.—Ten stages of ovarian development in *Engraulis mordax* based on modal length of the most advanced oocytes and the length interval containing the mode.

Stage of ovarian development	Location of mode of advanced oocytes (mm)	Stage of ovarian development	Location of mode of advanced oocytes (mm)
1	<0.20	6	0.60-0.68
2	0.20-0.28	7	0.70-0.78
3	0.30-0.38	8	0.80-0.88
4	0.40-0.48	9	0.90-0.98
5	0.50-0.58	10	>1.00

Fecundity estimates were based on counts of only the largest and most advanced oocytes (varying with stage of ovarian development) in three, wet weighed subsamples from the central region of the left, preserved ovary. Chi-square tests of independence indicated no significant difference ($P>0.05$) in oocyte size-frequency distribution among three different regions, anterior, central, and posterior, within the left ovary or between the central regions of either ovary. Each subsample, consisting of a clump of oocytes, was lifted from the ovary with a forceps and weighed to the nearest 0.1 mg. Subsample weights ranged from 10 to 50 mg. Oocyte counts were made under a dissecting microscope after the subsample had been teased apart in water. Each subsample yielded an estimate of fecundity expressed as total number of advanced oocytes contained in the ovaries, number of advanced oocytes per gram total body weight, and number of advanced ooctyes per gram ovary-free body weight. The mean of these subsamples provided the fecundity estimate for each

of 21 northern anchovies. Functional (geometric mean) regressions (Ricker 1973) were used to examine relationships between total fecundity and body weight (grams), standard length (millimeters), and ovary weight (grams). These regression equations can also be used for prediction of fecundity from body weight and standard length. The standard error of each (geometric mean) regression coefficient was obtained by taking the square root of the variance as calculated from Ricker (1973). Ricker also gave procedures to transform functional parameters to predictive if this is desired.

Photomicrographs of oocytes in various stages of development were taken at magnifications of 12.5, 21, or 25× through a dissecting microscope using transmitted light.

RESULTS

Length and Age at Sexual Maturity

Estimates of the size when northern anchovies reach sexual maturity were determined from observations of gonads from frozen fish collected in May (991 fish) and July (263 fish) 1975. Estimates of age were based on counts of annuli, the interface between an inner hyaline and outer opaque zone, on otoliths (Collins and Spratt 1969; Spratt 1975) but only data on ages I and II fish are reported here. Otoliths of anchovies collected in May and July with either a hyaline margin but no completed annulus or an annulus at the margin were considered to be age I. Northern anchovies from May and July with one completed annulus on their otoliths and a hyaline margin were considered to be age II.

All fish, <85 mm SL, taken in May (376) were immature. Both mature and immature fish were found within the size range 85-128 mm SL. Of 79 fish between 85 and 100 mm SL, 69% were immature and 31% were mature. Of 205 fish between 101 and 120 mm SL, only 5% were immature and 95% were mature. Only 3 out of 147 fish between 120 and 128 mm were immature and all fish >128 mm SL were mature.

Of 183 age I fish taken in May and measuring 55-99 mm SL ($\bar{x}$ = 75 mm SL) only 5 males, 84-96 mm SL, appeared to be mature. Yet of 263 age I fish measuring 56-94 mm SL ($\bar{x}$ = 76 mm SL), collected in July during the spawning season, none were mature. Possibly gametes begin to develop in adolescent northern anchovies early in the season but then do not reach the final stages of maturation required for spawning. Hickling (1930, 1935) reported this phenomenon in adolescent hake, *Merluccius merluccius*, from the North Atlantic. Of 14 age II northern anchovies from May (sex was not recorded), 7 were immature and 7 were mature. The smallest northern anchovies observed in spawning condition in July were 104 mm SL (male) and 107 mm SL (female). Ages are not available for these fish. This evidence indicates attainment of sexual maturity in some northern anchovies by age II.

Gonadal Condition

General gonadal development was measured in both immature and mature northern anchovies by mean monthly gonadal indices (Table 3). Mean GI's of immature males between 86 and 100 mm SL and females between 96 and 100 mm SL increased between March and May indicating some gonadal growth and differentiation. By July GI's in these size groups were lower than in May indicating no further gonadal development had occurred. Mean GI's of mature fish, >101 mm SL, increased from

TABLE 3.—Mean gonadal indices ($\overline{GI}$) by month for male (M) and female (F) *Engraulis mordax* in different size (standard length) intervals (N = no. of fish).

		81-85 mm		86-90 mm		91-95 mm		96-100 mm		101-110 mm		111-120 mm		121-130 mm		>131 mm	
Month	Item	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F
March	N	3	3	10	8	5	12	8	4	14	25	27	28	9	19	1	4
	$\overline{GI}$	0.22	1.12	0.25	0.99	0.20	1.08	0.36	1.20	0.48	1.18	0.68	1.24	1.22	1.55	0.64	1.70
May	N	9	9	4	7	9	6	5	2	23	9	20	6	10	9	16	36
	$\overline{GI}$	0.32	0.45	0.77	0.57	1.52	1.07	3.06	3.60	5.10	3.57	5.43	2.68	5.21	4.21	7.21	5.30
June	N	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	1
	$\overline{GI}$												4.77				5.64
July	N	11	4	9	3	4	8	3	2	7	4	26	15	38	23	13	21
	$\overline{GI}$	0.08	0.32	0.09	0.39	0.11	0.43	0.59	0.55	7.75	10.92	7.53	10.77	8.20	11.66	8.85	10.62
October	N	4	10	4	2	1	3	—	1	4	—	3	—	1	—	—	—
	$\overline{GI}$	0.07	0.52	0.05	0.50	0.04	0.40		0.43	0.11		0.18		0.14			

March through July. October GI's were the lowest values observed in mature fish. Only in May were the GI values of males higher than those of females. The highest mean GI's were observed in July, approximately midway through the spawning season, mid-June to mid-August, (Richardson 1973, footnote 5; Richardson and Pearcy 1977). The highest, 22.90 (female) and 15.39 (male), and lowest, 1.55 (female), individual values of the GI found in July indicated the presence of both running ripe and spent fish, respectively.

Sex Ratio

The male to female ratio of mature and immature northern anchovies before spawning in May; immature, nonspawning, fish in July; and mostly immature fish in October did not deviate significantly from 1:1 ($P>0.05$; chi-square test for goodness of fit) (Table 4). The sex ratio of 506 northern anchovies taken in March was 1.2:1 which, although close to 1:1, was significantly different ($P<0.05$). The overall male to female ratio of mature fish caught during active spawning in July at four different locations was 2.6:1. Values for each catch were 2:1 (167 fish), 8.3:1 (278 fish), 1:1 (186 fish), and 5.7:1 (40 fish). The sex ratios in those catches where males outnumbered females all deviated significantly from 1:1 ($P<0.005$) and may be related to anchovy spawning behavior. In the three catches where males greatly outnumbered females, the percent of ripe females with hydrated oocytes which were either actively spawning or about to spawn ranged from 33 to 46%. In the catch with a 1:1 sex ratio, only 2% of the females were ripe with ovaries full of hydrated oocytes.

TABLE 4.—Male to female ratios of northern anchovies collected in March, May, July, and October off Oregon and Washington.

Month	N	Male: female ratio	Size range (mm SL)
March	506	1.2:1	72-140
May	163	0.9:1	53-162
July:			
Nonspawning	247	1.2:1	56-94
Spawning	646	2.6:1	104-147
October	115	0.7:1	58-126

Ovarian Maturation

Oocyte Morphology

The smallest oocytes visible at 50× magnification were roughly spherical but by 0.20 mm were becoming elliptical in shape (Figure 2a). Most oocytes <0.38 mm lacked yolk and were transparent. Vitellogenesis became evident only in oocytes >0.38 mm. As yolk production continued, oocytes became more opaque and by 0.50 mm the nucleus was obscured. Most oocytes >0.50 mm were completely opaque, and oocytes between 0.50 and 0.68 appeared dark in transmitted light (Figure 2b). Oocytes between 0.70 and 0.90 mm often appeared less dense and dark than smaller yolked oocytes. A general lightening occurred first at the poles and then throughout the oocyte. These oocytes were grainy in appearance because globules of yolk had replaced the single amorphous yolk mass of smaller oocytes. The yolk of hydrated oocytes, ranging in size from 0.90 to 1.42 mm, was segmented (Figure 2c). Hydration, the accumulation of fluids of lower specific gravity than seawater in oocytes, results in greatly increased volumes and is the final stage of oocyte maturation in many marine fishes ([Fulton 1898] in Leary et al. 1975; Smith 1957). The largest oocytes (1.10-1.42 mm) in Figure 2c had been ovulated, i.e., released from their follicles, and were lying loose in the ovary. The shadowy areas among the opaque oocytes to the left of the transparent ones in this figure are empty follicles. These structures were dispersed throughout the ovary and were visible without the aid of histological techniques. They appeared as thin, flattened mats of tissue about the size and shape of ripe oocytes with a thinner, oval region in the center.

In addition to normally developing oocytes, degenerating or atretic oocytes were found in some anchovy ovaries collected before, during, and after the spawning season. Atresia has been observed in both immature oocytes undergoing vitellogenesis and mature oocytes remaining in the ovary after spawning in many teleosts (Wallace 1903; Matthews 1938; Hoar 1955; Vladykov 1956; Beach 1959; Barr 1968). Degenerating oocytes of all sizes in *E. mordax* most frequently appeared as opaque, irregularly shaped, masses dispersed among the normal yolked and yolkless oocytes (Figure 3a). Another type of abnormal and presumably degenerating oocyte was found primarily in fish with ripe oocytes. These medium-sized, 0.36-0.54 mm, oocytes were in early stages of vitellogenesis and had irregularly shaped nuclei which frequently appeared partially collapsed (Figure 3b). Within

[5]Richardson, S. L. 1977. Abundance, distribution and seasonality of larval fishes collected 2 to 11 km of Yaquina Bay, Oregon from January 1971-August 1972—a data summary. Oreg. State Univ. Sea Grant Coll. Prog. Publ. ORESU-T-77-003, 73 p.

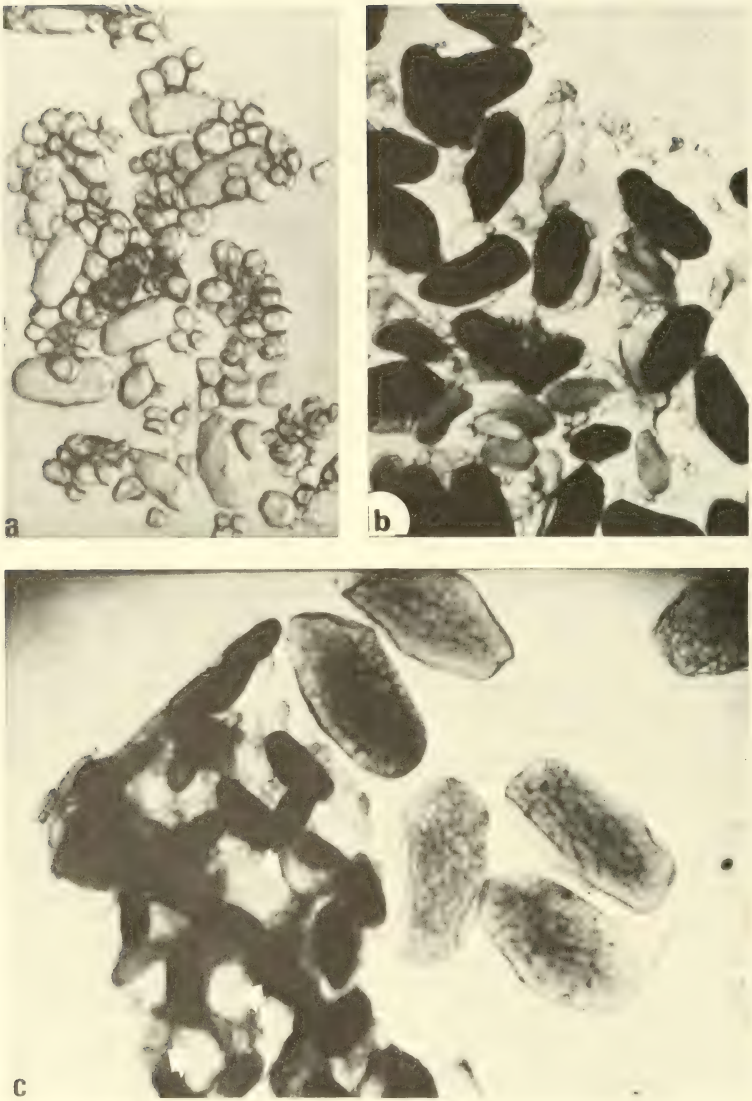


FIGURE 2.—Photomicrographs of normally developing, ovarian oocytes from *Engraulis mordax*. a. Yolkless oocytes, ranging from 0.14 to 0.28 mm length, from a northern anchovy captured in March (×25). b. Yolked (opaque) and yolkless (transparent) oocytes from a northern anchovy captured in June (×12.5). c. Ovulated oocytes (right) and empty follicles (arrows left) from a northern anchovy captured in July (×12.5).

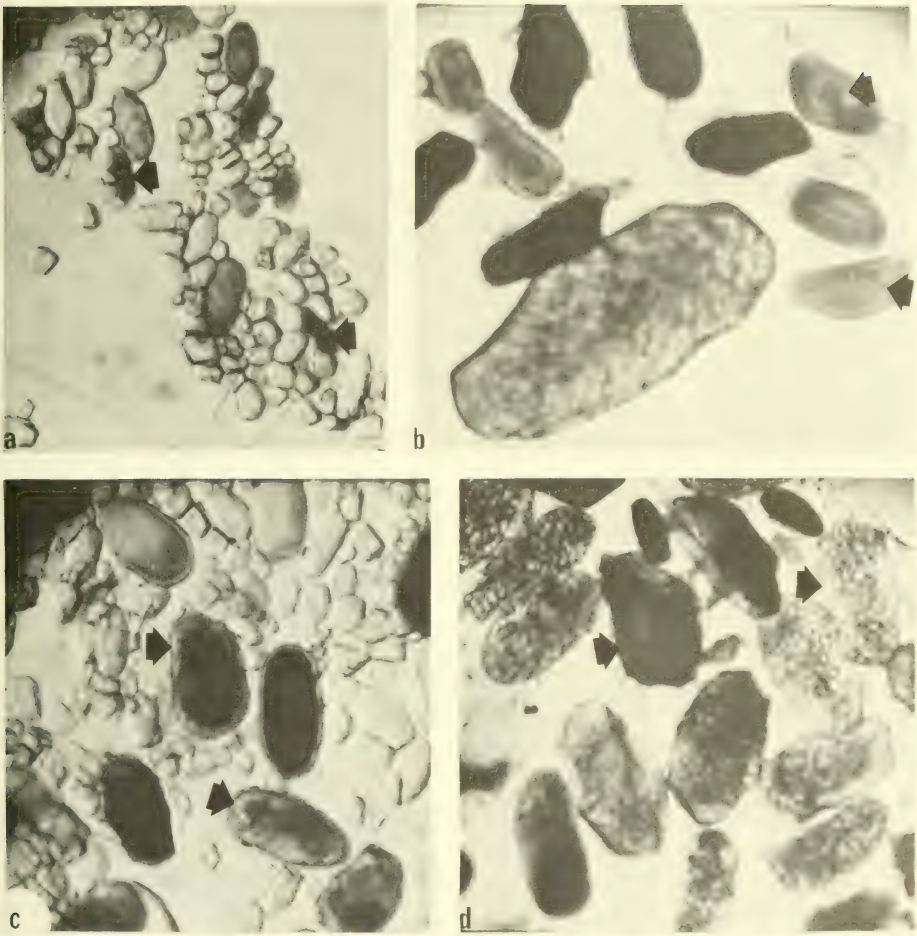


FIGURE 3.—Photomicrographs of degenerating ovarian oocytes from *Engraulis mordax*. a. Degenerating oocytes (arrows) from a northern anchovy captured in July (×25). b. Degenerating oocytes with abnormal nuclei (arrows) from a ripe northern anchovy captured in July (×25). c. Degenerating oocytes (arrows) from a northern anchovy captured in May (×25). d. Degenerating ripe oocytes (arrows) from a northern anchovy captured in July (×12.5).

more mature, degenerating oocytes the yolk appeared mottled and often the outline of the oocyte was irregular (Figure 3c). Ripe, ovulated oocytes that were degenerating differed from normal ones primarily in the appearance of the yolk. Instead of the honeycomblike, segmented yolk of normal oocytes, yolk in degenerating, ripe oocytes was either a solid opaque mass, or was dispersed into individual globules that looked like oil droplets (Figure 3d).

Oocyte Size-Frequency Distributions

Oocyte growth was traced through the composite size-frequency curves of 51 northern anchovies, representing nine stages of ovarian development,

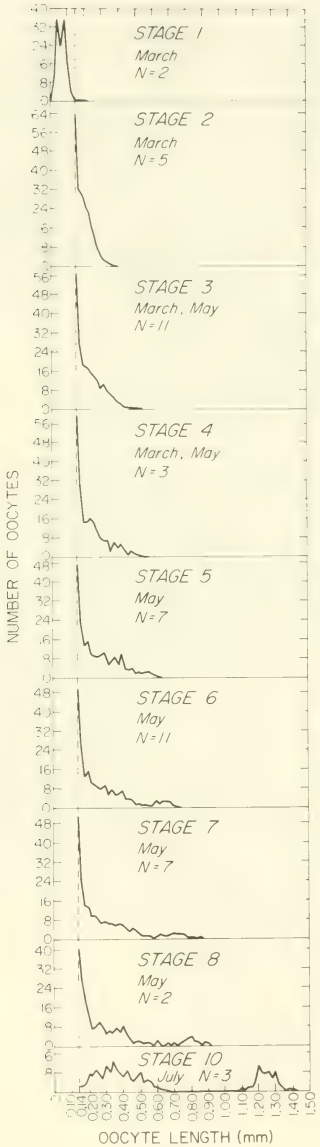


FIGURE 4.—Composite oocyte size-frequency curves representing nine stages of ovarian development in *Engraulis mordax*. (*N* = no. of fish.)

that were arranged in increasing order of maturity (Figure 4). Only fish taken in March and May before the spawning season were used for the curves of stages 1-8, although fish in these stages were taken in other months. Stage 10 fish, characterized by the presence of hydrated oocytes, were taken only in July. Few oocytes in the 0.90-0.98 mm size range were seen and no stage 9 fish were found. This apparent break in size distribution was caused by rapid hydration of oocytes during final maturation to ripe oocytes >0.90 mm. The increase in oocyte size during hydration is illustrated by the comparison of oocyte size distributions in stage 10 fish before and after ovulation (the release of oocytes from their follicles just prior to spawning) (Figure 5).

The most mature group of oocytes first began to form a distinct mode in stage 4 ovaries. Secondary modes of early yolked oocytes also appeared in stage 4 and were present in stages 5 through 10 but one of these groups never separated from the yolkless oocytes to form a distinct intermediate mode. These same groups of early yolked oocytes, especially the mode between 0.45 and 0.50 mm, were in essentially the same position in the oocyte size distributions of spent and ovulated stage 10 fish (Figure 5).

At least two stages of oocyte maturation prior to hydration were indicated by two modes in the size-frequency distributions of all completely opaque oocytes in weighed subsamples from two

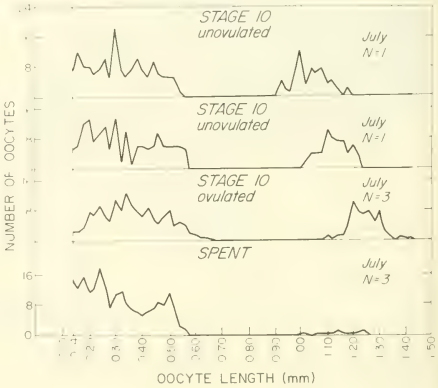


FIGURE 5.—Composite oocyte size-frequency curves from northern anchovies in ovarian stage 10, before and after ovulation, and in spent condition. (*N* = no. of fish.)

mature northern anchovies (130 and 141 mm SL) captured in July (Figure 6). Four maturation stages among yolked oocytes were found in *E. japonicus* after inspection of histological preparations, a more precise method, which were found to coincide with stages of ovarian development based on oocyte size composition (Usami 1963). At 50× magnification the general appearance of oocytes from the two mature, northern anchovies was the same but inspection of the size distributions indicated two groups. In the 130 mm fish, two modes of oocytes were apparent but not distinctly separate. But in the 141 mm fish, after additional growth the mode of larger oocytes became distinct and were probably ready to undergo hydration and ovulation subsequent to spawning.

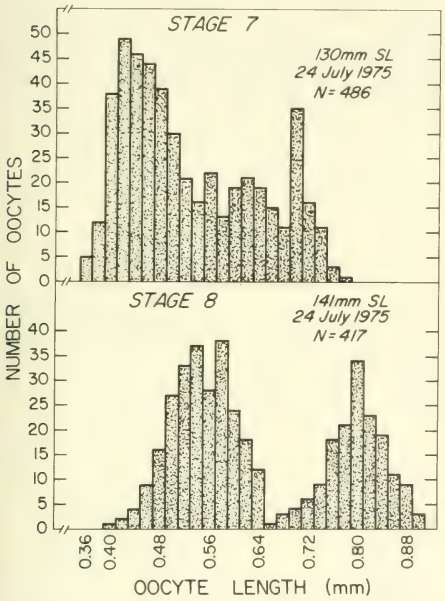


FIGURE 6.—Size-frequency histograms of all completely opaque oocytes in weighed subsamples from two northern anchovies, one in ovarian stage 7 and one in ovarian stage 8. (N = total number of oocytes measured.)

Fecundity

Estimates of fecundity were made on only the ripest northern anchovies, ovarian stages 6-10, captured in July during the spawning season when recruitment of yolked oocytes to the most advanced mode was nearly complete (Table 5). Fish in stages 6-8 used for fecundity determinations had not spawned recently as evidenced by the absence of empty follicles or degenerating ripe oocytes in their ovaries. Oocytes in stage 10 fish had not been ovulated yet; therefore, none had been lost because of spawning or handling during capture.

The mean total fecundity of 21 northern anchovies was 16,826±1,563 oocytes, and mean relative fecundity was 720±40 oocytes/g total body weight or 826±49 oocytes/g ovary-free body

TABLE 5.—Data for 21 female northern anchovies, *Engraulis mordax*, collected off the Oregon-Washington coast in July 1975-77 used to estimate fecundity. Gonadal index (1) and relative fecundity (1) were calculated using body weight + ovary weight. Gonadal index (2) and relative fecundity (2) were calculated using ovary-free body weight.

Collection year	Standard length (mm)	Body weight (g)	Ovary weight (g)	Gonadal index (1)	Gonadal index (2)	Ovarian stage	Total fecundity	Relative fecundity (1)	Relative fecundity (2)	Size range of advanced oocytes (mm)
1975	130	23.83	1.1733	4.92	5.18	7	10,409	437	459	≈0.56-0.78
	141	28.60	2.1407	7.48	8.09	8	14,561	510	550	0.68-0.90
1976	110	16.07	0.9072	5.65	5.98	6	9,514	592	628	0.58-0.70
	129	24.24	1.8615	7.68	8.32	7	20,766	857	928	0.60-0.76
1977	115	17.86	3.2030	17.93	21.85	10	12,426	696	848	1.13-1.40
	117	16.33	1.5167	9.29	10.24	7-8	17,039	1,044	1,151	0.63-0.83
	117	21.11	4.8348	22.90	29.70	10	17,712	839	1,088	1.08-1.33
	118	15.47	0.8538	5.52	5.84	7	8,694	562	595	0.63-0.78
	120	20.29	1.0179	5.02	5.28	7-8	12,294	606	638	0.65-0.83
	120	18.57	2.8745	15.48	18.30	10	10,922	588	696	1.18-1.38
	120	20.22	2.5489	12.61	14.43	10	8,673	429	491	1.13-1.38
	120	17.77	3.3445	18.82	23.18	10	13,813	777	957	0.95-1.25
	124	22.68	3.6194	15.96	18.99	10	15,089	665	792	1.03-1.23
	124	21.60	3.3617	15.56	18.43	10	13,369	630	733	1.02-1.22
	127	23.63	1.7524	7.42	8.01	7-8	19,451	823	889	0.68-0.85
	127	23.44	4.7776	20.38	25.60	10	19,623	837	1,052	1.03-1.28
	128	23.57	1.0465	4.44	4.65	6-7	14,157	601	629	0.60-0.78
	133	29.90	5.9563	20.84	24.88	10	22,012	736	919	1.05-1.31
	139	30.37	2.2317	7.35	7.93	7	28,235	929	1,003	0.63-0.75
	140	31.37	6.2765	20.01	25.02	10	29,035	926	1,157	0.92-1.18
	147	34.53	3.2000	9.27	10.21	7-8	35,561	1,030	1,135	0.68-0.85

weight (Table 6). These two expressions of relative fecundity were calculated to allow comparisons with results of previous studies and to illustrate how each method might bias fecundity estimates. Mean relative fecundity based on total body weight of fish in ovarian stages 6-8 and 10 was similar. But mean relative fecundity based on ovary-free body weight in these two groups differed by nearly 100 oocytes. Because oocyte hydration substantially increases ovary weight in ripe fish, the best (least biased) estimate of mean relative fecundity, when individual estimates are based on fish captured both prior to and after oocyte hydration, is ooctyes per unit ovary-free body weight. Yet either expression of relative fecundity can be biased if there are changes in somatic weight associated with the reproductive cycle or changes in condition, i.e., the length-weight relationship from year-to-year or among geographical regions (Bagenal 1967).

Linear and exponential (based on $\log_{10}$ transformed variates) expressions yielded similar fits to the relationship between fecundity (*TF*) and total body weight (*W*) and between *TF* and standard length (SL) with *r* values ranging from 0.73 to 0.82 (Table 7). The linear equations describing the relationship between *TF* and ovary weight (*OVW*) also yielded high *r* values, 0.92 for stages 6-8 fish and 0.96 for stage 10 fish. The apparent difference between the slopes of these two equations, 11,506.73 for stages 6-8 and 4,637.89 for stage 10, can be explained by the substantial increase in ovary weight in stage 10 fish caused by oocyte hydration, and not by an actual decrease in number of oocytes in these fish. Fecundity would be underestimated if an equation relating *TF* to *OVW* in fish with hydrated oocytes was used to predict fecundity. The relationship between *TF* and *OVW*, if based on fish captured both prior to and after oocyte hydration, would yield a low correlation coefficient (*r*).

TABLE 6.—Mean fecundity (± SE) of *Engraulis mordax* collected off the Oregon-Washington coast. Total fecundity = number of advanced oocytes in ovaries; relative fecundity = (1) number advanced oocytes per gram total body weight (ovary weight included) and (2) number advanced oocytes per gram ovary-free body weight.

Classification	Ovarian stages 6-8 (11 fish)	Ovarian stage 10 (10 fish)	Ovarian stages 6-10 (21 fish)
Total fecundity	17,335±2,525	16,267±1,881	16,826±1,563
Relative fecundity (1)	726±65	712±43	720±40
Relative fecundity (2)	782±75	873±63	826±49

TABLE 7.—Functional (geometric mean) regression equations, sample size (*N*), standard error of the regression coefficient (SE), and correlation coefficient (*r*) for the relationship between total fecundity (*TF*) and total body weight (*W*), standard length (*SL*), and ovary weight (*OVW*) in *Engraulis mordax* collected off the Oregon-Washington coast.

Equations	*N*	SE	*r*
Ovarian stages 6-10:			
$TF = -13.889.91 + 1,339.57W$	21	176.54	0.82
$\log_{10} TF = 1.91 + 1.69 \log_{10} W$	21	0.24	0.77
$TF = -76,286.31 + 738.99\ SL$	21	108.56	0.77
$\log_{10} TF = -6.80 + 5.23 \log_{10} SL$	21	0.82	0.73
Ovarian stages 6-8:			
$TF = -1,181.63 + 11,506.73\ OVW$	11	1,534.23	0.92
Ovarian stage 10:			
$TF = -2,654.20 + 4,637.89\ OVW$	10	433.83	0.96

Spawning Frequency

The number of times a female anchovy in the northern subpopulation spawns during the year could not be determined directly with available data. Oocyte observations, however, provided some information pertinent to the question of spawning frequency in these fish.

Degenerating, immature, yolked oocytes (those with abnormal-looking nuclei) were found in ripe northern anchovies during the spawning season. Although relative numbers of these oocytes were not determined, their presence suggests that oocytes in early stages of vitellogenesis in July may eventually degenerate and be absorbed. Higham and Nicholson (1964) also found disintegrating intermediate and maturing oocytes in the ovaries of recently spent Atlantic menhaden, *Brevoortia tyrannus*, indicating perhaps that this species may also absorb immature, yolked oocytes after spawning.

The presence of a distinct, intermediate mode of oocytes, indicating simultaneous maturation of a new batch of oocytes while a group of advanced oocytes is still in the ovary, is considered to be strong evidence of multiple spawning (Clark 1929; MacGregor 1976). In the oocyte size distributions of mature northern anchovies an intermediate mode of yolked oocytes never became distinctly separate from the smaller, yolkless oocytes (Figure 5). There was some indication of continued growth among intermediate-sized, yolked oocytes (0.56-0.66 mm) in five stage 10 fish (both unovulated and ovulated) before spawning. Yet oocytes in this size range were absent in three spent fish (Figure 5). The mode of intermediate-sized, yolked oocytes at 0.50 mm in these spent fish was in essentially the same position as in stage 10 (ovulated) fish, indicating little additional oocyte growth for some un-

determined period of time after spawning (Figure 5). Similarly shaped oocyte size distributions were used as indirect evidence of a single seasonal spawning in the Hawaiian anchovy, *Stolephorus purpureus* (Leary et al. 1975), the anchoveta, *Cetengraulis mysticetus* (Howard and Landa 1958), and the Pacific and jack mackerels, *Scomber japonicus* and *Trachurus symmetricus* (MacGregor 1976).

A secondary batch of oocytes, numerically equal to the group of hydrated oocytes about to be spawned was not found in stage 10 fish. The number of intermediate-sized, 0.46-0.62 mm, yolked oocytes, the next most advanced oocytes in ovaries of all stage 10 fish, was 427 oocytes/g ovary-free body weight (mean of three subsamples) in a 154 mm SL, stage 10 anchovy. This value, expressed as an estimate of relative fecundity, was about one-half the value of mean relative fecundity of ten stage 10 fish (Table 6) and lay outside the range of all 21 individual fecundity estimates (Table 5).

DISCUSSION

Length and Age at First Maturity

Published reports of size and age at first maturity of anchovies in the central subpopulation are somewhat conflicting. Clark and Phillips (1952) found that only 30% of the fish in the size range 100-120 mm SL (ages I and II) were mature and only 50% in the size range 120-139 mm SL (ages II and III) were mature. Yet Huppert et al. (footnote 3) reported a recent study that found all northern anchovies older than 24 mo, ≈120 mm SL, to be mature.

Sexual maturity is also attained in nothern anchovies of the northern subpopulation at the end of the second year. Pike (1951) found that 96% of the northern anchovies in the size range 105-109 mm SL (age II fish), from commercial catches, were mature while only 14% of the fish ranging from 100 to 104 mm SL (<2 yr old) were mature. Northern anchovies off Oregon similarly do not attain sexual maturity until after the second year (i.e., in the third summer). The smallest northern anchovies taken in this study in spawning condition were 104 mm SL (male) and 107 mm SL (female). Size at maturity seems to be somewhat smaller in the northern subpopulation, possibly reflecting differences in growth rates between the two subpopulations.

Sex Ratio

It appears that the overall sex ratio in both the central and northern subpopulations is ≈1:1. Klingbeil (1978) reported that the overall male to female ratio of northern anchovies from sea survey samples off California combined for the years 1966-75 was 0.97:1. Monthly sex ratios in commercial catches from February to August off British Columbia were approximately 1:1 with females slightly outnumbering males (0.77:1 the lowest ratio) (Pike 1951). The male to female ratio of both mature and immature anchovies off Oregon before the spawning season (May) and immature fish during and after the spawning (July and October) was also about 1:1.

Yet samples from both central and northern subpopulations were found with unexpectedly higher numbers of either males or females. Klingbeil (1978) suggested that adult northern anchovies may often be segregated by sex, although no seasonal trends could be discerned in their data. Hunter and Goldberg (1980) found that in trawl collections of northern anchovies off California dominated by males, 40% of the females had spawned on the night of capture. But in female dominated collections only about 10% of the females had spawned the night of capture. They suggested that changing sex ratios in northern anchovy schools may be associated with reproductive behavior. The overall male to female ratio of mature fish caught in July in areas of active spawning off Oregon and Washington was 2.6:1, with sex ratios in individual catches ranging from 1:1 to 8:1. The highest male to female ratios were also associated with catches containing high numbers of ripe females which were or soon would be spawning. The percent of these ripe females in male dominated schools off Oregon and Washington ranged from 33 to 40% and was similar to the percent of most recently spawned females in male dominated schools off California (Hunter and Goldberg 1980). Pike (1951) found that the relative number of male anchovies increased as the spawning season approached and in July males slightly outnumbered females. But by August, at the end of the spawning season, the male to female ratio was 0.71:1.

Fecundity

The only previous estimate of northern anchovy fecundity in the northern subpopulation,

1,369±148 oocytes/g total body weight (n = 4) (Pike 1951), differs from our estimate of 720±40 oocytes/g total body weight (n = 21). Our estimate is more accurate than Pike's because it is based on counts of only the most advanced oocytes in ripe or nearly ripe fish. Pike's fecundity estimate was based on the assumption that northern anchovies spawn three equal batches of oocytes per year and was calculated by dividing the total number of oocytes >0.20 mm by three. His assumption of spawning frequency, based on the number of modal peaks in oocyte size-frequency distributions, is still unproven and could lead to erroneous fecundity estimates depending on the actual number of spawnings per fish.

Northern anchovies in the northern subpopulation off Oregon and Washington apparently have a greater fecundity (based on ovary-free body weight), 826 (n = 21), than those in the central subpopulation off California, based on estimates by MacGregor (1968) and Hunter and Goldberg (1980), 606 (n = 19) and 389 (n = 23), respectively. An analysis of variance (single classification) indicated the presence of a highly significant ($P<0.01$) added variance component between individual relative fecundity estimates (based on ovary-free body weight) of our fish and those examined by MacGregor (1968). Hunter and Goldberg's mean value, which is more directly comparable than MacGregor's with our estimate because it was similarly based on ripe fish with hydrated oocytes, was even lower than MacGregor's, although statistical comparisons were not possible (individual fecundity values were not listed). The difference between the two California estimates may have been due primarily to differences in the stage of ovarian maturation of the fish used for fecundity determinations. Difficulty in distinguishing the most mature oocytes from less mature ones before hydration could have caused the higher estimate obtained by MacGregor who used only fish with unhydrated oocytes.

The higher fecundity of northern anchovies off Oregon and Washington may represent a true racial difference between fish in the northern and central subpopulations. Racial differences in fecundity have been demonstrated in many species of fish with probable causes being either environmental or genetic factors (Bagenal 1957, 1967). Bagenal (1966) speculated that geographic differences in plaice fecundity were caused by differences in food availability and population density.

Spawning Frequency

Fish, such as the northern anchovy, with asynchronous oocyte development have the potential to spawn more than once during the season (de Vlaming 1974). Yet the actual number of times a female northern anchovy spawns during a year has not been conclusively documented in any of the subpopulations. Pike (1951) estimated that northern anchovies in the northern subpopulation off British Columbia spawn three times during the 3-mo spawning season. MacGregor (1968) suggested that at least some fish in the central subpopulation spawn more than once during the spawning season, which may include all 12 mo of the year. Hunter and Goldberg (1980) estimated the spawning frequency of northern anchovies in the central subpopulation to be once every 6-7 d during months of peak spawning.

Pike's (1951) conclusion was based solely on the presence of multiple modes in oocyte size distributions and ambiguous data on changes in the ratio of immature to advanced oocytes during the spawning season. These data alone cannot be used to determine spawning frequency in fishes. MacGregor (1968) concluded that spawning later in the year represented repeat spawning by some northern anchovies because early in the spawning season all mature females had well-developed eggs or were recently spent. Christiansen and Cousseau (1971), using histological techniques, found that some female *M. merluccius* had the physiological ability to recover more rapidly after spawning than the rest of the population and that these fish spawned a second time later in the season off Argentina. It seems likely, therefore, that anchovies in the central subpopulation spawn more than once during the protracted spawning season. But the number of spawnings per year may be variable because environmental conditions such as temperature and food supply, which are known to influence reproductive cycling in fishes, can vary from year to year (Bagenal 1966, 1969; de Vlaming 1971, 1974; Hodder 1972; Tyler and Dunn 1976). Recently, Brewer (1978) suggested that food availability may limit both the number of eggs spawned and the number of spawnings per year by northern anchovies in San Pedro Bay, Calif.

Hunter and Goldberg's (1980) estimate of spawning frequency was based on the mean percent incidence of northern anchovies with 1-d-old ovarian follicles in trawl samples taken during a 2-wk period in February. Their determination of

spawning frequency depended on the, as yet, unproven assumption that all mature females in the central subpopulation spawn during 1 mo of the peak spawning period. Even if this assumption is correct the dependence of this method on obtaining samples which accurately reflect the proportion of spawning and nonspawning females in the population poses another problem. Spawning frequency will be overestimated if nonspawning females are not as susceptible as spawning fish to capture by sampling gear because of differences in spatial distribution or behavior of the two groups.

Our oocyte observations alone, without data on rates of oocyte maturation and degeneration, did not yield an estimate of northern anchovy spawning frequency in the northern subpopulation. But our findings indicated that oocyte degeneration and apparent reduced growth among intermediate-sized, yolked oocytes prior to and after release of one batch of oocytes may limit the number of subsequent spawnings. In addition, the actual length of the spawning season off Oregon and Washington is only 2 mo, although water temperatures favorable for northern anchovy spawning (13°-17.5° C at 10 m depth, Baxter 1967) are present in this region for 5-6 mo. This discrepancy supports our interpretation of the oocyte observations by indicating that environmental factors may not be suitable for complete maturation of all yolked oocytes present in northern anchovy ovaries in the northern subpopulation. Only data from laboratory experiments designed to determine rates of oocyte maturation (and degeneration) under varying environmental conditions, such as photoperiod, temperature, and food supply, will provide a definitive answer to the question of how many times northern anchovies spawn per year.

Seasonal Distribution Associated with Reproduction

A distinct geographic segregation of mature and immature northern anchovies and hence an inferred spawning migration during the summertime spawning season occurs in the northern subpopulation off Washington, Oregon, and northern California but apparently not around British Columbia. Evidence for this resulted from a summary of data from a number of sources including data and cruise reports (Table 8), Tillman,[6] and personal observations from our own sampling efforts (Table 1, Figure 1). These seasonal patterns in the northern subpopulation, described here for the first time, were evident even though the data were obtained with various types of sampling gear and unequal sampling effort.

In winter, January through March, both mature and immature northern anchovies of all sizes (≈50-180 mm) occur in nearshore coastal areas off British Columbia, Washington, and Oregon. Small schools were seen in British Columbia coastal waters. Concentrations were found off Washington between Cape Flattery and Destruction Island (over 31-313 m depths) and between Grays Harbor and the Columbia River (42-101 m depths). Off Oregon, northern anchovies were taken between the Columbia River and Coos Bay (91-183 m depths) with largest numbers occurring between the Columbia River and Tillamook Bay. Fish off Washington and Oregon were observed or captured near the bottom or in midwater in coastal areas, but were not commonly taken in bays and estuaries. Small catches of fish were taken in the Strait of Juan de Fuca but none were taken in Puget Sound, Wash.; Yaquina Bay, Oreg; or Humboldt Bay, Calif. A few rare occurrences (50-70 mm FL) have been reported from Tillamook Bay, Oreg.

In spring, April through mid-June, northern anchovies still occur in nearshore coastal waters. Fish, 80-160 mm SL, were taken in the seine fishery of the 1940's in British Columbia coastal waters. Although no schools were observed off the northern Washington coast, northern anchovies, 50-170 mm SL, were consistently taken near the bottom or in midwater in the vicinity of the Columbia River mouth (20-91 m depth). Northern anchovies, mostly <100 mm, were collected in the spring in Tillamook Bay, Yaquina Bay, and Coos Bay, Oreg. (sizes not given). Northern anchovies of all sizes entered Humboldt Bay in April and remained there into June and July.

In summer, mid-June through September, both mature and immature anchovies (up to 160 mm SL) occur in nearshore coastal waters of British Columbia where they supported a major seine fishery in the 1940's. Although few ripe or spent adults were taken, spawning is reported to occur in bays and inlets around southern British Columbia in summer. Off Washington and Oregon, sexually mature and immature northern anchovies are geographically separated. Adult fish

[6]M. F. Tillman, Northwest and Alaska Fisheries Center Marine Mammal Division, NMFS, NOAA, 7600 Sand Point Way NE, Seattle, WA 98115, pers. commun. April 1975.

TABLE 8.—Summary of additional studies in which juvenile and adult *Engraulis mordax* from the northern subpopulation were collected.

General area	Dates	Principal gear	Sampling effort	Reference
British Columbia, bays and inlets	1940-50; mostly Feb.-Sept. 1947 and June-July 1948	Commercial purse seine	40 random samples	Pike (1951)
British Columbia, Saanich Inlet	23 Apr.-21 July 1968	6 m surface trawl	weekly, 116 tows	Barraclough et al.[1]
British Columbia, Strait of Georgia	4-6 July 1967	6 m surface trawl	24 tows	Robinson[2]
Puget Sound, Strait of Juan de Fuca, Washington coast from Mukkaw Bay to Columbia River (15-220 fm)	10-28 Jan. 1966	Standard Cobb pelagic trawl and 2/3 scale Cobb pelagic trawl (echosounder used to locate fish schools)	19 tows	BCF exploratory cruise no. 75, RV *John N. Cobb*[3]
Washington coast between Cape Flattery and Columbia River (10-140 fm)	6 Apr.-4 May 1966	Standard Cobb pelagic trawl and 2/3 scale Cobb pelagic trawl (echosounder used to locate fish schools)	6 tows	BCF exploratory cruise no. 77, RV *John N. Cobb*[3]
Washington coast between Cape Flattery and Destruction Island (20-100 fm) and between Grays Harbor and Columbia River (10-50 fm)	8-18 Nov. 1966	2/3 scale Cobb pelagic trawl (echosounder used to locate fish schools)	2 tows	BCF exploratory cruise no. 82, RV *John N. Cobb*[3]
Washington-Oregon coast between Cape Flattery and Yaquina Bay	18 Nov.-16 Dec. 1966 and 3 Jan.-8 Apr. 1967	Standard Cobb pelagic trawl, 2/3 scale Cobb pelagic trawl, and 2 experimental anchovy trawls (echosounder used to locate fish schools)	71 tows (most tows made in Jan.-Apr.)	BCF gear research cruise no. 8, MV *Baron*[3]
Washington-Oregon coast between Cape Flattery and Heceta Head (15-100 fm)	15 May-2 June 1967	BCF Universal trawl (echosounder used to locate fish schools)	7 tows	BCF exploratory cruise no. 87, RV *John N. Cobb*[3]
Tillamook Bay, Oreg.	May 1974-May 1976	6 m try net; 46 m beach seine	≈biweekly, then monthly	Forsberg et al.[4]
Yaquina Bay, Oreg.	July 1964-Sept. 1967	6 m otter trawl (plus other gear)	≈monthly	Beardsley (1969)
Coos Bay, Oreg.	June-Sept. 1970	61 m beach seine; 30 m bag seine (plus other gear)	Not specified	Cummings and Schwartz[5]
Humboldt Bay, Calif.	Apr. 1974-Oct. 1976	Echosounder—to determine distribution of anchovy schools; 200 m lampara bait seine 66.7 × 6.7 m purse seine (plus other gear)	Weekly echosounder surveys plus 45 net hauls	Waldvogel (1977)

[1]Barraclough, W. E., D. G. Robinson, and J. D. Fulton. 1968. Data record—Number, size composition, weight, and food of larval and juvenile fish caught with a two-boat surface trawl in Saanich Inlet April 23-July 21, 1968. Fish. Res. Board Can., Manuscr. Rep. Ser. 1004, 305 p.

[2]Robinson, D. G. 1969. Data record—Number, size composition, weight and food of larval and juvenile fish caught with a two-boat surface trawl in the Strait of Georgia July 4-6, 1967. Fish. Res. Board Can., Manuscr. Rep. Ser. 1012, 71 p.

[3]Information from cruise reports, Northwest and Alaska Fisheries Center, NMFS, NOAA, 2725 Montlake Blvd. East, Seattle, WA 98112.

[4]Forsberg, B. O., J. A. Johnson, and S. M. Klug. 1977. Identification, distribution, and notes on food habits of fish and shellfish in Tillamook Bay, Oregon. Oreg. Dep. Fish Wildl. Res. Sec., Fed. Aid Prog. Rep. Fish. 1977, 117 p.

[5]Cummings, E., and E. Schwartz. 1971. Fish in Coos Bay, Oregon, with comments on distribution, temperature, and salinity of the estuary. Oreg. Dep. Fish Wildl., Coastal rivers invest.—Inf. Rep. 70-11, 22 p.

in spawning condition were found offshore with main concentrations between lat. 43° and 47° N and ≈65-157 km offshore. They occurred in small schools near the surface at night and deeper in the water column during daylight. Immature fish (mostly <100 mm SL) remained in nearshore coastal areas or in bays. They were taken in Grays Harbor, Wash., around the Columbia River mouth, in Tillamook Bay, Yaquina Bay, and Coos Bay, where they were observed feeding at the surface during daylight. In Humboldt Bay, mature fish left in June and July leaving only immature fish in the bay through the summer. Adults presumably moved offshore to spawn, although it is not known whether they moved north off Oregon and Washington or elsewhere. Adults returned to the bay around mid-September in spent condition.

In fall, October through December, northern anchovies are no longer abundant around British Columbia. The fishery of the 1940's was generally not in operation that season. Off Washington and Oregon, adults eventually return to coastal waters from offshore spawning areas although few adults were collected in the fall. Fall catches occurred mainly off the Columbia River mouth (13-61 m depth) and Grays Harbor (35-37 m depth). Immature fish appeared to leave the bays and estuaries and returned to nearshore coastal waters. Young fish were seen in the Columbia River in October, feeding at the surface. No anchovies were collected in Tillamook Bay, Yaquina Bay, or Coos Bay. Juveniles and adults left Humboldt Bay in late October-November.

A pronounced and well-defined onshore-offshore segregation of mature and immature fish and inferred offshore spawning migration during the spawning period as observed in the northern subpopulation off Washington, Oregon, and northern California has not been documented for northern anchovies in the central or southern subpopulations. Baxter (1967) stated that off California northern anchovies apparently move offshore in

fall and winter, during the peak spawning period, and return inshore in spring. Huppert et al. (footnote 3) indicated similar movements but provided little additional information. Brewer (1978) suggested that mature northern anchovies in the vicinity of San Pedro Bay move to deeper, cooler waters offshore to spawn. The distinct geographic segregation of mature and immature northern anchovies in the northern subpopulation which occurs because of an offshore migration of spawning fish may represent an additional racial difference among the three northern anchovy subpopulations in the northeast Pacific.

ACKNOWLEDGMENTS

Wayne A. Laroche took the photomicrographs of oocytes. Jerome D. Spratt and John S. Sunada of the California Department of Fish and Game checked our otolith readings and provided useful advice concerning interpretation of northern anchovy age data. Percy L. Donaghay gave us many helpful ideas for data analyses and Rae Deane Leatham generously provided assistance with all computer work. David L. Stein rendered a careful review of the manuscript. John R. Hunter, National Marine Fisheries Service (NMFS), La Jolla, read an earlier version of the manuscript and suggested useful ways to improve it. The following individuals helped us during this study by providing information on the location of northern anchovies at sea or collected and saved fish for us: P. Killian, W. Nichols, and G. Muhlberg of the Clatsop Community College, Astoria, Oreg.; M. Hosie, G. Hettman, J. Lukas, and B. Forsberg of the Oregon Department of Fish and Wildlife; T. Durkin, NMFS, Hammond, Oreg.; W. Pearcy, D. Stein, and E. Krygier of the Oregon State University, Corvallis, Oreg.

This work is a result of research sponsored by the Oregon State University Sea Grant College Program, supported by NOAA Office of Sea Grant, Department of Commerce, under Grant No. 04-6-158-44094.

LITERATURE CITED

BAGENAL, T. B.
1957. Annual variations in fish fecundity. J. Mar. Biol. Assoc. U.K. 36:377-382.
1966. The ecological and geographical aspects of the fecundity of the plaice. J. Mar. Biol. Assoc. U.K. 46:161-186.
1967. A short review of fish fecundity. *In* S. D. Gerking (editor), The biological basis of freshwater fish production, p. 89-111. Wiley, N.Y.
1969. The relationship between food supply and fecundity in brown trout *Salmo trutta* L. J. Fish Biol. 1:167-182.

BARR, W. A.
1968. Patterns in ovarian activity. *In* E. J. W. Barrington and C. Barker Jorgensen (editors), Perspectives in endocrinology, p. 163-238. Acad. Press, N.Y.

BAXTER, J. L.
1967. Summary of biological information on the northern anchovy, *Engraulis mordax* Girard. Calif. Coop. Oceanic Fish. Invest. Rep. 11:110-116.

BEACH, A. W.
1959. Seasonal changes in the cytology of the ovary and of the pituitary gland of the goldfish. Can. J. Zool. 37:615-625.

BEARDSLEY, A. J.
1969. Movement and angler use of four foodfishes in Yaquina Bay, Oregon. Ph.D. Thesis, Oregon State Univ., Corvallis, 148 p.

BREWER, G. D.
1978. Reproduction and spawning of the northern anchovy, *Engraulis mordax*, in San Pedro Bay, California. Calif. Fish Game 64:175-184.

CHRISTIANSEN, H. E., AND M. B. COUSSEAU.
1971. Reproduction of the hake in the Argentine Sea. 2. Hake reproduction and its relationship with other biological aspects of the species. Bol. Inst. Biol. Mar. Del Plata 20:43-75. (Translated from Span. by Fish. Mar. Serv. Transl. Ser. 4003, 1977.)

CLARK, F. N.
1929. The life history of the California jack smelt, *Atherinopsis californiensis*. Calif. Div. Fish Game, Fish Bull. 16, 22 p.
1934. Maturity of the California sardine (*Sardina caerulea*), determined by ova diameter measurements. Calif. Div. Fish Game, Fish Bull. 42, 49 p.

CLARK, F. N., AND J. B. PHILLIPS.
1952. The northern anchovy (*Engraulis mordax*) in the California fishery. Calif. Fish Game 38:189-207.

COLLINS, R. A., AND J. D. SPRATT.
1969. Age determination of northern anchovies, *Engraulis mordax* from otoliths. *In* J. D. Messersmith (editor), The northern anchovy (*Engraulis mordax*) and its fishery 1965-1968, p. 37-55. Calif. Dep. Fish Game, Fish Bull. 147.

DE VLAMING, V. L.
1971. The effects of food deprivation and salinity changes on reproductive function in the estuarine gobiid fish, *Gillichthys mirabilis*. Biol. Bull. (Woods Hole) 141:458-471.
1974. Environmental and endocrine control of teleost reproduction. *In* C. B. Schreck (editor), Control of sex in fishes, p. 13-83. Va. Polytech. Inst. State Univ., Blacksburg, Sea Grant Publ. VPI-SG-74-01.

FULTON, T. W.
1898. On the growth and maturation of the ovarian eggs of teleostean fishes. 16th Annu. Rep. Fish. Board Scotl. Part III:88-124.

HART, J. L.
1973. Pacific fishes of Canada. Fish. Res. Board Can., Bull. 180, 740 p.

HICKLING, C. F.
1930. The natural history of the hake. Part III. Seasonal changes in the condition of the hake. Fish. Invest. Minist. Agric. Fish. (G.B.), Ser. II, 12, 78 p.

1935. Seasonal changes in the ovary of the immature hake, *Merlucius merluccius* L. J. Mar. Biol. Assoc. U.K., New Ser., 20:443-461.

HIGHAM, J. R., AND W. R. NICHOLSON.
1964. Sexual maturation and spawning of Atlantic menhaden. U.S. Fish Wildl. Serv., Fish. Bull. 63:255-271.

HOAR, W. S.
1955. Reproduction in teleost fish. *In* I. Chester Jones and P. Eckstein (editors), The comparative physiology of reproduction and the effects of sex hormones in vertebrates, p. 5-22. Mem. Soc. Endocrinol. 4.

HODDER, V. M.
1972. The fecundity of herring in some parts of the Newfoundland area. Int. Comm. Northwest Atl. Fish., Res. Bull. 9:99-107.

HOWARD, G. V., AND A. LANDA.
1958. A study of the age, growth, sexual maturity and spawning of the anchoveta (*Cetengraulis mysticetus*) in the Gulf of Panama. Inter-Am. Trop. Tuna Comm. Bull. 2:391-467.

HUNTER, J. R., AND S. R. GOLDBERG.
1980. Spawning incidence and batch fecundity in northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 77:641-652.

KLINGBEIL, R. A.
1978. Sex ratios of the northern anchovy, *Engraulis mordax*, off Southern California. Calif. Fish Game 64:200-209.

LAGLER, K. F.
1956. Freshwater fishery biology. Wm. C. Brown Co., Dubuque, Iowa, 421 p.

LEARY, D. F., G. I. MURPHY, AND M. MILLER.
1975. Fecundity and length at first spawning of the Hawaiian anchovy, or Nehu (*Stolephorus purpureus* Fowler) in Kaneohe Bay, Oahu. Pac. Sci. 29:171-180.

MACGREGOR, J. S.
1968. Fecundity of the northern anchovy, *Engraulis mordax* Girard. Calif. Fish Game 54:281-288.
1976. Ovarian development and fecundity of five species of California Current fishes. Calif. Coop. Oceanic Fish. Invest. Rep. 18:181-188.

MCHUGH, J. L.
1951. Meristic variations and populations of northern anchovy (*Engraulis mordax mordax*). Bull. Scripps Inst. Oceanogr., Univ. Calif. 6:123-160.

MATTHEWS, S. A.
1938. The seasonal cycle in the gonads of *Fundulus*. Biol. Bull. (Woods Hole) 75:66-74.

MILLER, D. J., AND R. N. LEA.
1972. Guide to the coastal marine fishes of California. Calif. Dep. Fish Game, Fish Bull. 157, 235 p.

PIKE, G. C.
1951. Age, growth and maturity studies on the Pacific anchovy (*Engraulis mordax*) from the coast of British Columbia. M.A. Thesis, Univ. British Columbia, Vancouver, Can., 44 p.

RICHARDSON, S. L.
1973. Abundance and distribution of larval fishes in waters off Oregon, May-October 1969, with special emphasis on the northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 71:697-711.
In press. Spawning biomass and early life of northern anchovy, *Engraulis mordax*, in the northern subpopulation off Oregon and Washington. Fish. Bull., U.S. 78(4).

RICHARDSON, S. L., AND W. G. PEARCY.
1977. Coastal and oceanic fish larvae in an area of upwelling off Yaquina Bay, Oregon. Fish. Bull., U.S. 75:125-145.

RICKER, W. E.
1973. Linear regressions in fishery research. J. Fish. Res. Board Can. 30:409-434.

SMITH, S.
1957. Early development and hatching. *In* M. E. Brown (editor), The physiology of fishes, Vol. 1, p. 323-359. Acad. Press, N.Y.

SPRATT, J. D.
1975. Growth rate of the northern anchovy, *Engraulis mordax*, in southern California waters, calculated from otoliths. Calif. Fish Game 61:116-126.

TYLER, A. V., AND R. S. DUNN.
1976. Ration, growth, and measures of somatic and organ condition in relation to meal frequency in winter flounder, *Pseudopleuronectes americanus*, with hypotheses regarding population homeostasis. J. Fish. Res. Board Can. 33:63-75.

USAMI, S.
1963. Fecundity of the Japanese anchovy, *Engraulis japonica* (Houttuyn)—II. Histological study on the ovarian egg of the anchovy in Mutsu Bay. [In Jpn., Engl. synop.] Bull. Tokai Reg. Fish. Res. Lab. 37:1-9.

VLADYKOV, V. D.
1956. Fecundity of speckled trout (*Salvelinus fontinalis*) in Quebec Lakes. J. Fish. Res. Board Can. 13:799-841.

WALDVOGEL, J. B.
1977. Age, maturity and distribution of northern anchovy, *Engraulis mordax*, in Humboldt Bay, California. M.S. Thesis, Humboldt State Univ., Arcata, Calif., 36 p.

WALLACE, W.
1903. Observations on ovarian ova and follicles in certain teleostean and elasmobranch fishes. Q. J. Microsc. Sci., New Ser. 47:161-214.

DIETS OF FOURTEEN SPECIES OF VERTICALLY MIGRATING MESOPELAGIC FISHES IN HAWAIIAN WATERS

THOMAS A. CLARKE[1]

ABSTRACT

Fishes and zooplankton were sampled at four depths (70, 90, 110, 170 m) at night in the upper layers near Hawaii. Diets of the fishes were determined from stomach contents and preferences estimated by comparison with prey densities at the appropriate depth. Generally, the fishes fed on relatively large, pigmented or opaque crustaceans; other taxa and very small or translucent prey were rarely eaten. There were, however, differences in diet and preference between species; these were frequently correlated with morphological features, especially lens size and gill raker spacing. One group of four fishes which were very similar in both diet and morphology were separated by depth distribution and size. Comparison with other studies indicates that tropical species are perhaps more specialized and ecologically separated in diet than their counterparts in high latitudes.

Vertically migrating mesopelagic fishes are important components of oceanic ecosytems. In the tropical open ocean, abundance of larvae (Ahlstrom 1969) and estimates of biomass (Clarke 1973; Maynard et al. 1975) indicate that they are the dominant group of micronekton and greatly exceed the abundance of epipelagic forms. Standing crops are even higher in oceanic situations at higher latitudes (Frost and McCrone 1979) and coastal upwelling areas (Pearcy and Laurs 1966). Tropical oceanic faunas are much more diverse. At high latitudes and in quasi-neritic situations, one to three species typically make up the great majority of the standing crop (Pearcy and Laurs 1966; Zahuranec and Pugh 1971; Baird et al. 1975; Frost and McCrone 1979), while in the tropical open ocean the abundances of the dozens of cooccurring species are more evenly distributed (Clarke 1973, 1974).

The diets of these fishes are of interest both to assess their impact on lower trophic levels in oceanic ecosystems and to determine the degree to which cooccurring species are specialized with respect to their feeding habits; however, previous studies do not allow serious consideration of these aspects. Few have presented extensive data on more than one to three species. For the most part, prey have not been identified adequately enough to seriously discuss preference or dietary overlap, and there has been no consideration of bias due to differing rates of digestibility and, therefore, ability to identify different prey types (Gannon 1976). Few studies have compared stomach contents of fishes with appropriate samples of the prey available; those that have done so have simply compared percentages of different prey types and have not considered biases or errors inherent in the samples taken for prey abundance.

This paper considers diets of 14 species of vertically migrating mesopelagic fishes based on data from collections taken near Hawaii in the central North Pacific Ocean. All species are primarily zooplanktivorous and are known (Clarke 1978) or suspected to feed principally in the upper 250 m at night. The diets of each species are compared with densities of zooplankton at each of the depths sampled. While problems in feeding studies mentioned above have by no means been completely eliminated, the methodology recognizes and at least qualitatively attempts to account for major sources of error. The results allow consideration of biases of the fishes as "samplers" of the potentially available prey and of dietary overlap between species or sizes cooccurring at the same depths in the water column.

METHODS

Field Collections

All specimens for this study were collected ca. 20 km off the coast of Oahu, Hawaii, (ca. lat. 21°10′-30′ N, long. 158°10′-30′ W) over bottom depths of 2,000-4,000 m. The depth ranges, vertical migra-

[1]University of Hawaii, Department of Oceanography and Hawaii Institute of Marine Biology, P.O. Box 1346, Kaneohe, HI 96744.

Manuscript accepted January 1980.
FISHERY BULLETIN: VOL. 78, NO. 3, 1980.

tions, and other aspects of the ecology of the species considered have been reported for the same study area (Clarke 1973; Clarke and Wagner 1976) and other studies there summarized by Maynard et al. (1975).

Fishes were collected with a 3 m (10-ft) Isaacs-Kidd midwater trawl. To minimize the probability of fishes' feeding while in the net, the terminal section of the net was of ca. 3 mm knotless nylon mesh instead of the commonly used, finer plankton netting.

The trawl was launched and towed at ca. 2 m/s and the ship was slowed to ca. 1 m/s for retrieval. Total time for descent to and ascent from towing depth was 12-20 min. The trawl was towed at the desired depth for ca. 2 h. Zooplankton were sampled with 70 cm diameter, opening-closing bongo nets of 505 μm mesh. Ship's speed of ca. 1 m/s was maintained for the entire tow; the nets were open at the desired depth for 30-33 min. Time-depth recorders attached to the nets indicated that the depths of the "horizontal" (2 h) portions of the trawl tows and the open part of the bongo net tows were within 5 m of each other and of the desired depth for each set of samples. All collections were preserved in ca. 5% formaldehyde in seawater solution immediately after the nets were on deck.

Four different depths (70, 90, 110, 170 m) were sampled (Table 1). In September 1973, two plankton tows followed by two trawl tows were made on the same night at each of three depths (70, 110, and 170 m). For the 170 m collections the bongo nets failed to open and close properly on one of the tows. A single trawl sample from 90 m was taken in November 1974, and a single plankton sample taken at the same depth two nights later. All tows were taken between last light at dusk and first light at dawn and within 2 d of new moon. Thus ambient light was essentially constant for all samples taken at a given depth, and there were probably no between-sample differences in vertical distribution of either the fishes or their prey at a given depth. Consequently, except for possible captures in transit to and from towing depth (see below), the fishes captured at a given depth were assumed to have been feeding on the same prey population sampled by the appropriate plankton tows.

TABLE 1.—Sampling information for trawl and plankton collections at four different depths off Oahu, Hawaii. D + R = total time for descent and retrieval of trawl.

Depth (m)	Trawl			Plankton net	
	Date	Time at depth[1]	D + R (min)	Date	Time open at depth[1]
70	24-25 Sept. 1973	2158-2400	13	24 Sept. 1973	2010-2040
	25 Sept. 1973	0045-0245	12	24 Sept. 1973	2101-2131
90	11-12 Nov. 1974	2300-0100	18	14 Nov. 1974	2353-0023
110	26 Sept. 1973	0007-0207	13	25 Sept. 1973	2202-2235
	26 Sept. 1973	0237-0437	15	25 Sept. 1973	2256-2328
170	26-27 Sept. 1973	2318-0118	15	26 Sept. 1973	1953-2030
	27 Sept. 1973	0150-0350	20		

[1]Hawaii standard time.

Laboratory Procedures

All nonlarval fishes from the trawls were identified and standard length (SL) measured to the nearest millimeter. The fishes from each depth were grouped by species and arbitrary size classes: 16-25 mm, 26-35 mm, 36-45 mm, 45-60 mm, and >61 mm. Certain species or size classes from each depth were eliminated from consideration because, based on previous evidence of depth-size distributions (Clarke 1973; Clarke and Wagner 1976), they were almost certainly taken in transit to and from towing depth. Among the size classes that were considered, a few possibly included specimens that were captured above towing depth and thus were not exposed to the same array of prey as sampled by the plankton nets; these groups are noted specifically in subsequent sections.

For each specimen examined, standard length was recorded and the stomach (anterior end of the esophagus to the pyloric constriction) removed. Prey items with bodies intact were noted separately and measured to the nearest 0.1 mm with an ocular micrometer. For the commonly occurring crustacean prey, the following measurements were used: copepods—prosome length, ostracods—maximum carapace length, malacostracans—the distance from the anteriormost point exclusive of the antennae to the base of the telson. (The telson of malacostracans was too frequently separated to routinely include it in the length.) The dimensions measured for other intact prey were standard length for fishes, maximum diameter for nearly spherical items such as gastropod veligers, and total length for all others. Most intact copepods and euphausiids could be indentified to genus and most copepodite VI stages of the former and juveniles and adults of the latter to species. Ostracods were almost all *Conchoecia* spp., but were not identified further. Other prey types were identified only to major taxa. Identifiable frag-

ments of digested prey among the remainder of the stomach contents were also recorded.

Prey items in the mouth were discarded, but items in the esophagus were included with the stomach contents. The bodies of items in the esophagus were compressed and the appendages were flattened against the body. Such items could conceivably have been eaten in the trawl, but several lines of evidence indicate that this is an unimportant source of error. Hopkins and Baird (1975) reported no evidence of net feeding even when a fine mesh cod end (which would presumably accumulate more zooplankton and restrict water flow) was used. Only a few of the species considered here had items in the esophagus at all frequently, and in all cases such items were the same or very similar to items frequently found among digested or partially digested matter in the stomach. Thus if there was significant net feeding, only some species did so and apparently selected prey from that in the cod end similar to their normal habits.

The species-size groups for which data are presented here are those from which a reasonable number of intact prey were recorded. If sufficient numbers of specimens were available, I examined specimens until about 100 intact items were recorded. For other groups, I examined all the fish collected, but eliminated from consideration those for which too few prey items were recorded either because of low numbers of specimens or low incidence of prey in the stomach.

Zooplankton from the bongo net samples were identified and counted from aliquots taken with a plankton splitter. Euphausiids and most adult copepods were identified to species—the former from between all and one-eighth of the sample and the latter from one-sixteenth to one-thirtysecond. Most immature copepods were identified to genus. Ostracods and amphipods from one-sixteenth to one-thirtysecond of the sample were counted and measured to the nearest 0.1 mm. Other taxa were counted from all to one-eighth of the sample. Flowmeters on the plankton nets gave suspect readings; consequently, volumes sampled by each tow were calculated from the duration of the open part of the tow and estimated speed (1 m/s). The densities (per cubic meter) of the different prey types were calculated from the volumes and adjusted counts.

The apparent search volume per fish (ASV) was used as an index of relative preference for the different prey types. For each type of prey noted from the stomachs of each category of fish, the ratio of the total number of intact items to the density of that type was divided by the number of fish with intact items in the stomach. Fish examined but with no intact prey items in the stomach were eliminated because they provided no information on preference, they included fish that had not fed at all as well as those with variable amounts of digested material in the stomach, and finally their proportion of the total fish examined varied between categories. Thus the ASV's as calculated here apply to fish that had fed recently before capture and take no account of between-category differences in feeding success.

The ASV is the minimum volume the average fish of each category had to search to capture the observed number of a given prey type. The actual volume searched is larger to the extent that the fish are not 100% effective in detecting, capturing, and ingesting prey. If the fish were equally effective in detecting, capturing, and ingesting all types of prey, the ASV's would be equal. For a given category of fish, differences in ASV's between prey types indicate the degree to which the fish were "biased samplers" of the available prey and thus measure relative preference in the broadest sense, i.e., without specifying which aspects of predation were biased.

The ASV is similar to the index of preference recently derived by Chesson (1978); the relationship between the two indices is:

$$\alpha_i = \frac{V_i}{\sum_{k=1}^{m} V_k}$$

where for type i out of m prey types, V_i is the ASV and α_i is Chesson's index. Unlike ASV, α has no dimensions and is normalized. Assuming that predation does not substantially alter prey densities, i.e., that the number of prey eaten is low relative to the total available, both indices are equivalently related to the probability of a given type of prey being eaten:

$$P_i = \frac{V_i \rho_i}{\sum_{k=1}^{m} V_k \rho_k} = \frac{\alpha_i n_i}{\sum_{j=1}^{m} \alpha_j n_j}$$

where P_i is the probability of prey type i being eaten, and p_i and n_i are the density and number of

prey type i available. Like α, the ASV is unaffected by negative or positive preference for other types of prey. As pointed out by Chesson (1978), most other indices of preference, including that of Ivlev (1961), are so affected and their biological meaning is not clear.

Preference could be affected by many characteristics of the prey, only one of which could be considered in this study. Other things being equal, large or more visible prey types could be detected at greater distances (Zaret and Kerfoot 1975; O'Brien et al. 1976) and thus have higher ASV's than small or translucent types. Consequently, in addition to measuring size of prey, I examined several samples of living zooplankton from the study area and noted, for as many prey types as possible, whether they were opaque or translucent in life and the presence of any pigment.

Ability to escape once detected and attacked would decrease ASV. Prey with bioluminescent organs could either be more readily detected than those without or conceivably use them to decrease probability of detection or capture. Aggregation or patchiness of prey could also affect ASV either way depending upon patch size, predator capacity, and the search behavior of the predator. Unfortunately, none of these behavioral aspects of predation could be investigated.

For each of the fish species considered here, I examined four morphological features which could affect preference. Relevant measurements were made to the nearest 0.1 mm with either an ocular micrometer or vernier calipers on at least five specimens spanning the size range of each species considered. The length of the premaxillary was taken as a measure of gape; the diameter of the lens, as a measure of visual ability; and the average space between gill rakers on the lower branch of the first arch, as a measure of minimum particle size that could be retained. These were expressed as linear functions of standard length determined by least squares regression. The filtering area of the gill rakers, which could not be directly calculated without knowledge of the angle at which the arch is held during feeding, was assumed proportional to the product of the length of the raker-bearing segments of the first arch and the length of the gill raker at the joint between the upper and lower branches. This product or "area" was expressed as a power function of standard length determined by linear squares regression on the logarithms.

Aside from being affected by characteristics of the fishes and their prey, ASV's could have been biased by problems in the methodology. Any feeding in the net (considered above) would tend to increase ASV for large prey retained there and also blur any differences in visibility or escape behavior. Differential rates of digestion and disintegration of prey would bias stomach content data toward more resistant and more easily recognizable prey (Gannon 1976). Counting only intact and measurable prey eliminated bias due to differential ease of identification. For example, if all identifiable parts had been counted, the data would have been heavily biased toward *Pleuromamma* spp. whose spots or "buttons" can be recognized even after the items have completely disintegrated and passed into the intestine, while certain other prey which cannot be identified positively if only one or two features are missing would have been underrepresented. Even among the crustaceans, the rate at which the prey disintegrates probably varies; Gorelova (1975) indicated that some small cyclopoid copepods remain intact even in the intestine of myctophids. Other types of prey are probably digested much faster than crustaceans. To at least qualitatively correct for the latter bias, I counted all recognizable remains of chaetognaths, heteropods, other gastropods, siphonophores, and tunicates as "intact" for calculation of ASV's.

The densities of small zooplankton were underestimated due to escapement through the 505 μm mesh of the plankton nets used. Counts of ostracods and certain copepods from an available plankton tow from the study area with 333 μm mesh on one frame and 505 μm on the other indicated that—assuming that the 333 μm sampled the small prey accurately—prey >1 mm long were adequately retained by the 505 μm net. These included most of the prey eaten by the fishes. Two types of frequently eaten prey, large (0.6-0.8 mm) *Oncaea* spp. and ostracods <1.0 mm were underestimated by factors of roughly 4 and 5, respectively, in the 505 μm sample, and their ASV's are overestimated by the same factors. There were insufficient numbers of other small prey types in the 333/505 sample to provide even roughly reliable estimates of error.

Any avoidance of the bongo nets by prey would result in erroneously high estimates of ASV. No studies have documented the extent of error due to avoidance by different prey types, but it can probably be assumed to be negligible for the great

majority of prey types eaten by the fishes considered here. Certain types, e.g., large (>10 mm) euphausiids, shrimps, or fish larvae, must certainly be able to avoid the bongo nets; consequently, high ASV's associated with such types must be considered as doubtful.

Uncertainty associated with the estimated densities from the plankton tows probably limits interpretation more than any other factor. Since only one or two pairs of zooplankton samples were available from each depth, the sampling error associated with estimated densities cannot be specified. Overall, the between tow, between net, and between aliquot differences in counts of abundant types indicated that the densities and therefore the ASV's are probably accurate to within a factor of 0.5-2× of the values given. Thus small differences in ASV's cannot be considered real. Absurdly high values of ASV frequently resulted for prey types that were very rare or absent in the plankton samples. Such types were frequently large forms that may have been "rare" because of net avoidance, and even for those that were truly rare, the potential sampling error was probably large due to insufficient volumes sampled. Consequently, after inspection of the data, all values >1.0 m^3 were lumped together.

RESULTS

A total of 14 species of fishes comprising 51 size-depth-species categories (Table 2) yielded sufficient data to merit presentation and discussion. Although most prey items were identified to genus or species and all were measured to the nearest 0.1 mm, certain prey were grouped by higher taxa or size ranges for presentation of prey densities (Table 3) and to avoid dealing with low numbers in calculations of ASV's.

In the individual species accounts below, an attempt is made to summarize the major points in the tabulated data. For these purposes and subsequently throughout the paper, "microzooplankton" are operationally defined as those prey types too small (<1.0 mm) to have been accurately sampled by the plankton tows and thus those whose ASV's are overestimated. The remaining prey types or "macrozooplankton" are considered by species or as small (1.0-1.5 mm), medium (1.5-3.0 mm), or large (≥3.0 mm). For each category of fishes considered, the number of macrozooplankton prey types and their frequencies in the diet are grouped by ASV values in 0.1 m^3 increments between 0 and 1.0 m^3 (Table 2).

Lampanyctus steinbecki (Table 4)

The data for *L. steinbecki* are the most extensive of all species considered. Large numbers of at least two size classes were taken at each of the four depths sampled, and, in spite of the rather low numbers of prey per fish, the numbers identified for most categories were relatively high. The 18-25 mm fish from 90 and 110 m and 36-45 mm fish from 170 m may have included some individuals caught in transit above the towing depth.

Microplankton were of minor importance in the diets of all but the smallest size groups considered. Small macrozooplankton were eaten infrequently and had low ASV's for all sizes of fish. The most frequently taken prey were euphausiids and medium to large copepods. The ASV's for these and other large prey were usually relatively high. *Candacia longimana* was most consistent in this respect. The ASV's for *Pleuromamma xiphias* at 90 m were markedly lower than at the other depths as were those for *Euphausia* spp. at 70 m. Neither of these exceptions appeared to result from differences in importance in the diet. *Pleuromamma xiphias* was extremely abundant at 90 m (Table 3), and this, combined with the lower numbers of prey per fish at this depth, caused most of the reduction in ASV. *Euphausia* spp. were extremely abundant at 70 m (Table 3); most were *E. tenera*, a species eaten infrequently. As a consequence of these and similar differences between depths, there was no clear trend or consistency to the distribution of ASV's of the different prey types. Most types and most items had low ASV's at 90 m, ASV's were more nearly evenly distributed at 70 and 110 m, and the majority of prey had high ASV's at 170 m (Table 2).

Lampanyctus nobilis (Table 5)

Lampanyctus nobilis was taken from three depths; with the possible exception of the smallest size group from 110 m, the data were unlikely to have been seriously affected by catches in transit to and from towing depth.

The diet of *L. nobilis* was generally similar to that of *L. steinbecki* but with a greater frequency of large prey. Microzooplankton were hardly eaten (Table 2), and ASV's for the few types of small macrozooplankton were very low. The most fre-

TABLE 2.—Number of identified prey items, percentage of prey items <1.0 mm long, and distribution of types and percentages of prey items as a function of apparent search volume (see text) for each species, depth, and size category of fish examined. Given under each interval of apparent search volume are the number of types of macrozooplankton prey and, in parentheses, the percentage of total prey items whose apparent search volumes were in that interval.

Species, depth, standard length	No. prey items (% <1.0 mm)	Apparent search volume (m^3)										
		0-0.10	0.11-0.20	0.21-0.30	0.31-0.40	0.41-0.50	0.51-0.60	0.61-0.70	0.71-0.80	0.81-0.90	0.91-1.0	>1.0
Lampanyctus steinbecki:												
70 m: 26-35 mm	44(14)	3(20)	3(14)	1(5)	1(2)	1(23)	—	2(9)	—	—	1(9)	2(5)
36-45 mm	33	3(24)	1(3)	3(9)	1(3)	—	2(30)	—	—	—	1(9)	3(21)
46-52 mm	16	—	1(37)	—	1(6)	—	—	1(6)	1(37)	—	1(13)	—
90 m: 18-25 mm	17(35)	3(24)	2(18)	—	2(18)	—	—	1(6)	—	—	—	—
26-35 mm	37(14)	9(35)	3(19)	1(11)	2(14)	1(8)	—	—	—	—	—	—
36-45 mm	99 (6)	15(48)	3(14)	—	1(12)	1(6)	—	—	—	—	1(13)	—
46-51 mm	11 (9)	1(9)	2(27)	2(18)	—	—	1(9)	—	1(9)	—	—	1(18)
110 m: 19-25 mm	17	1(12)	3(24)	—	3(35)	1(6)	1(24)	—	—	—	—	—
26-35 mm	47(21)	6(17)	—	2(11)	1(21)	—	1(11)	1(11)	—	—	1(6)	1(2)
36-45 mm	133 (4)	4(5)	4(8)	1(4)	1(4)	1(7)	—	1(2)	1(34)	2(26)	—	2(7)
46-50 mm	69 (3)	6(12)	2(9)	2(3)	3(16)	2(51)	—	—	—	—	—	3(7)
170 m: 36-45 mm	40 (7)	2(5)	—	—	—	—	—	—	—	1(7)	—	8(80)
46-54 mm	89 (1)	5(8)	3(10)	—	—	1(3)	—	—	—	—	—	10(77)
L. nobilis:												
70 m: 36-45 mm	56 (4)	5(32)	6(18)	1(2)	—	1(4)	1(23)	1(2)	—	—	—	4(16)
47-57 mm	18	2(33)	2(11)	1(17)	—	—	—	—	—	1(6)	—	2(33)
64-78 mm	9	—	1(56)	1(11)	—	—	—	—	—	—	—	3(33)
90 m: 36-45 mm	45 (9)	4(22)	4(18)	2(7)	2(9)	1(13)	—	—	—	—	—	3(22)
46-60 mm	33	9(39)	1(6)	2(12)	—	1(6)	—	2(21)	—	—	—	4(15)
110 m: 37-45 mm	32	1(6)	3(9)	1(6)	2(25)	—	—	1(9)	1(16)	—	—	4(28)
47-60 mm	28	1(4)	3(1)	—	—	—	—	1(11)	1(36)	—	—	3(39)
62-75 mm	61	2(3)	2(5)	1(3)	—	1(7)	—	—	1(30)	—	1(2)	7(51)
76-86 mm	25	—	—	2(28)	—	—	2(20)	—	—	—	—	6(52)
Triphoturus nigrescens:												
70 m: 19-25 mm	108(44)	7(17)	1(2)	5(8)	1(13)	3(8)	—	1(3)	1(1)	1(2)	—	1(2)
26-37 mm	98(14)	12(31)	5(9)	3(4)	1(3)	4(6)	—	1(26)	1(5)	—	—	2(2)
Notolychnus valdiviae:												
90 m: 16-24 mm	51(51)	13(37)	1(2)	—	—	—	—	—	1(10)	—	—	—
110 m: 19-24 mm	136(57)	14(15)	3(15)	2(9)	1(1)	1(2)	—	—	—	—	—	—
170 m: 20-23 mm	89(25)	5(11)	2(2)	1(4)	3(8)	—	—	—	—	1(11)	—	5(38)
Ceratoscopelus warmingi:												
70 m: 46-69 mm	56(18)	6(21)	4(11)	2(4)	—	—	2(7)	1(2)	1(4)	—	—	7(34)
90 m: 38-45 mm	32(37)	4(22)	1(3)	3(16)	1(3)	—	—	1(6)	—	1(9)	—	1(3)
46-62 mm	153(20)	15(25)	5(18)	2(3)	2(4)	2(9)	2(3)	—	1(6)	—	1(5)	3(8)
110 m: 48-68 mm	53 (8)	1(4)	1(2)	3(9)	—	1(6)	—	—	—	—	1(13)	10(58)
Bolinichthys longipes:												
70 m: 17-26 mm	77(86)	3(4)	1(1)	—	3(6)	1(3)	—	—	—	—	—	—
90 m: 27-35 mm	125(86)	10(12)	2(2)	1(1)	—	—	—	—	—	—	—	—
36-47 mm	166(83)	12(10)	3(5)	1(1)	—	—	—	—	—	—	—	2(1)
110 m: 26-35 mm	236(88)	9(7)	2(2)	—	—	1(3)	—	—	—	—	—	—
36-49 mm	317(76)	8(3)	3(4)	1(1)	—	—	—	1(3)	—	—	1(5)	1(8)
Diogenichthys atlanticus:												
70 m: 17-21 mm	40(77)	4(10)	2(5)	—	1(3)	1(5)	—	—	—	—	—	—
Benthosema suborbitale:												
70 m: 18-25 mm	28(54)	4(14)	1(4)	1(4)	2(7)	—	—	2(11)	1(4)	—	—	1(4)
26-30 mm	69(42)	9(19)	4(13)	1(16)	1(4)	—	1(3)	—	—	—	—	1(3)
110 m: 26-32 mm	47(45)	4(13)	3(15)	2(23)	—	1(2)	—	—	—	—	1(2)	—
Diaphus schmidti:												
70 m: 31-35 mm	154(30)	1(5)	7(8)	—	2(10)	2(4)	1(1)	1(1)	—	—	—	10(42)
36-40 mm	120(39)	4(7)	5(8)	6(7)	2(18)	1(4)	1(1)	—	—	2(2)	1(2)	5(11)
90 m: 27-35 mm	180(49)	9(11)	4(4)	3(6)	—	2(5)	—	3(14)	—	—	1(1)	5(9)
36-41 mm	78(46)	5(15)	6(9)	4(14)	1(8)	—	—	1(4)	1(1)	—	—	2(3)
D. perspicillatus:												
70 m: 46-56 mm	418(33)	4(2)	2(3)	2(2)	—	2(3)	—	2(8)	—	2(2)	1(5)	16(41)
D. fragilis												
90 m: 34-44 mm	29(52)	2(7)	3(24)	2(7)	1(3)	—	—	—	—	1(3)	—	1(3)
D. trachops												
170 m: 36-50 mm	29(10)	—	2(10)	—	2(10)	1(3)	—	—	—	—	1(3)	7(62)
Melamphaes danae:												
70 m: 17-22 mm	54(22)	4(15)	5(22)	—	—	1(2)	2(18)	—	—	—	—	4(22)
90 m: 19-22 mm	31(23)	1(3)	2(26)	1(16)	—	1(16)	—	—	—	—	—	2(16)
110 m: 19-22 mm	34 (9)	—	1(6)	3(12)	—	—	—	—	—	1(21)	1(3)	7(50)
Bregmaceros japonicus:												
70 m: 38-51 mm	41 (2)	5(24)	1(5)	—	—	2(15)	2(39)	—	—	1(12)	—	1(2)

quent prey were euphausiids and *P. xiphias*; except at 70 m and 90 m, respectively, ASV's for these forms were relatively high. Generally ASV's of other large prey were also high.

Although there were no major between-depth differences in diet composition, ASV's were generally higher for fish from 110 m than for those from 70 and 90 m (Table 2). Among the fish from 110 m,

TABLE 3.—Density estimates of prey types at each of the four depths sampled. A "+" indicates presence, but with estimated density <0.005 m^{-3}. Undetermined subadult copepodite stages of copepods are designated by "C" and specific stages by "C" plus the appropriate Roman numeral; otherwise, copepods are all adults (CVI). Prey types <1.0 mm long, whose densities are probably underestimated due to mesh escapement, are starred.

Prey type	Density (m^{-3})				Prey type	Density (m^{-3})			
	70 m	90 m	110 m	170 m		70 m	90 m	110 m	170 m
Copepods:					Euphausiids:				
Neocalanus spp. CII, CIII	1.98	0.57	0.82	0.02	*Euphausia* spp.	6.40	0.30	0.52	0.01
Neocalanus spp. CIV, CV	0.62	0.42	0.23	0.05	*Stylocheiron* spp.	0.26	0.24	0.17	1.08
Neocalanus spp.	0.05	0.03	0.13	0.05	*Nematoscelis* spp.	0.02	0.01	0.07	1.17
Calanus tenuicornis	0.92	2.43	2.72	0.62	*Thysanopoda aequalis*	0.03	0.24	0.04	+
Nannocalanus minor	0.98	0.46	0.04	—	*Thysanopoda* spp.	0.01	—	0.02	+
Undinula vulgaris	0.08	0.02	—	—	*Nematobrachion sexspinosus*	—	+	+	+
U. darwini	0.12	0.36	0.01	—	Euphausiid larvae	0.44	0.24	0.11	0.07
Eucalanus spp.	0.06	0.02	0.02	0.01					
*Acrocalanus spp.	0.09	—	0.04	0.01					
*Clausocalanus spp.	1.26	1.11	2.45	0.47	Ostracods:				
*Pseudocalanidae	0.60	0.19	2.23	0.80	*- 1.0 mm	0.50	0.46	0.11	0.37
Euaetideus acutus	0.45	0.38	1.00	0.01	1.0-1.4 mm	1.40	1.67	0.60	1.18
Chiridius + *Gaetanus* spp.	—	0.35	0.15	0.17	1.5-1.9 mm	0.89	1.04	0.36	0.97
Aetideidae—C <2.0 mm	0.35	0.96	0.58	0.25	2.0-2.9 mm	0.09	0.19	0.04	0.09
Aetideidae—C 2.0-3.0 mm	0.28	0.96	1.02	0.22	≥ 3.0 mm	—	0.05	0.01	—
Aetideidae—CV, CVI >3.0 mm	0.27	0.59	0.55	0.08					
Euchaeta media	0.16	0.19	0.58	0.01	Amphipods:				
Euchaeta spp.	0.09	0.16	0.04	—	1.0-1.9 mm	0.49	0.35	0.13	0.07
Euchaeta spp. C ≤2.0 mm	0.11	0.68	0.92	0.39	2.0-2.9 mm	0.15	0.09	0.09	0.17
Euchaeta spp. C >2.0 mm	0.17	1.37	0.30	0.28	≥ 3.0 mm	0.03	0.03	0.07	0.12
Scolecithrix danae	0.08	0.03	+	—					
Scolecithrix bradyi	0.74	0.38	0.81	0.06	Caridean:				
*Scolecithricella spp. <1.0	0.45	0.32	0.23	0.35	juveniles and adults	+	+	+	+
Scolecithricella spp. ≥1.0	1.68	3.49	5.97	1.17	larvae	0.50	0.07	0.08	0.07
Lophothrix spp. CV, CVI	0.49	0.41	0.03	—					
Scottocalanus spp. CV, CVI	0.21	0.15	0.22	0.04	Penaeideans:				
Unident. Scolecithricidae/Phaennidae	0.23	0.36	0.35	0.14	juveniles and adults	0.02	0.03	0.02	0.01
Pleuromamma xiphias	1.29	5.01	1.42	0.43	larvae	0.03	0.05	0.01	—
P. xiphias CV	0.93	0.65	0.67	0.82					
P. abdominalis	0.34	0.63	0.49	0.09					
P. abdominalis C	3.87	0.38	0.81	1.82	Mysids	0.02	0.03	0.01	+
P. gracilis	2.57	2.37	5.34	1.42	Brachyuran zoeae	0.69	+	0.02	+
P. gracilis CV	0.72	0.65	0.68	0.72	Brachyuran megalopae	0.03	0.05	0.01	0.07
Centropages spp.	0.09	0.02	—	—	Anomuran larvae	0.02	—	0.01	0.03
Lucicutia sp.	0.74	0.35	0.31	0.99	Other crustacean larvae	—	+	+	+
Heterorhabdus papilliger	0.84	0.61	0.79	0.17	Chaetognaths	2.97	3.32	1.08	0.15
Heterorhabdus spp.	0.01	—	0.08	0.14	Larvaceans	0.14	0.76	0.17	—
Augaptilidae	0.16	0.24	0.29	3.38	Other tunicates	0.29	1.37	0.16	+
Candacia longimana	0.24	0.24	0.44	0.05	Siphonophores	0.71	1.26	0.12	0.01
Candacia spp. CV, CVI	0.34	0.93	0.51	0.41	Polychaetes	0.07	0.20	0.04	0.03
Paracandacia spp. CV, CVI	1.23	1.84	0.44	—	Heteropods	0.39	0.07	+	+
Pontellidae	0.01	—	—	—	*Gastropod larvae + pteropods <1.0 mm	2.82	0.21	0.17	0.03
Acartia spp.	0.38	0.22	0.44	0.01	*Pelecypod larvae	0.12	0.02	0.01	—
Unident. calanoids	0.13	—	—	0.07	Other invertebrate larvae	0.11	—	0.27	—
Oithona spp.	0.81	0.80	0.51	0.07	Miscellaneous	0.01	—	0.01	+
*Oncaea spp. >0.6 mm	0.54	0.53	0.60	1.00	Fish eggs	0.04	0.09	0.06	0.01
*Oncaea spp. ≤0.6 mm	0.04	—	0.01	0.22	Fish larvae	0.21	0.14	0.08	0.04
Corycaeus spp.	2.89	1.11	1.38	0.49					
Other cyclopoids	0.15	0.92	0.27	0.08					

there was a trend for higher ASV's in the larger fish; about half the prey taken by the two largest size groups had ASV's of 1.0 m^3 or more.

Triphoturus nigrescens (Table 6)

A large fraction of the diet of the smaller *T. nigrescens* were microzooplankton—mostly *Oncaea* spp. The most frequent prey among the macrozooplankton was *P. xiphias*; it and several other medium to large prey types had moderately high ASV's. Few prey had high ASV's and those with low ASV's included all sizes. If the ASV for *Oncaea* spp. is reduced by a factor of 4 to roughly correct for undersampling, it is still equal to or greater than those for the medium to large macrozooplankton. This indicates that preference for *Oncaea* by small *T. nigrescens* is similar to that for several larger prey types.

The microzooplankton were a small fraction of the diet of the larger *T. nigrescens*, and the corrected ASV for *Oncaea* spp. is relatively low. *Pleuromamma xiphias* was the most frequent prey species and had one of the higher ASV's. Most of the other prey were medium to large types, and some of these had moderate to high ASV's. The largest fraction of both items and prey types, however, had low ASV's (Table 2). These included both

TABLE 4.—Stomach contents of *Lampanyctus steinbecki*: number of fish examined, number with intact prey, total number of prey, and number of each prey type for each depth and size category. The apparent search volume (see text) for each prey type is given in parentheses after the number eaten. Rarely eaten prey types ("Other prey") are given by depth and size categories below the main body of the table. Copepodite stages of copepods are designated as in Table 3.

Depth	70 m			90 m				110 m				170 m	
Standard length, mm	26-35	36-45	46-52	18-25	26-35	36-45	46-51	19-25	26-35	36-45	46-50	36-45	46-54
No. examined	23	14	7	18	38	103	12	15	22	50	45	20	53
No. with intact prey	18	11	6	8	25	55	7	12	19	42	41	16	35
No. of intact prey	45	33	16	18	39	101	11	18	47	134	69	40	93
Prey type	No. (Apparent search volume, m³)												
Calanus tenuicornis	—	—	—	1(0.05)	1(0.02)	3(0.02)	—	—	2(0.04)	—	—	—	1(0.05)
Gaetanus spp.	—	—	—	—	—	1(0.10)	—	—	—	—	—	—	3(0.49)
Aetideidae C 2.0 mm	—	1(0.26)	—	—	—	1(0.02)	—	—	—	—	—	—	1(0.11)
Aetideidae C 2.0-3.0 mm	1(0.20)	1(0.33)	—	—	3(0.12)	3(0.06)	—	—	1(0.05)	3(0.07)	2(0.05)	3(0.86)	11(1.44)
Aetideidae CV, CVI >3.0 mm	3(0.61)	3(0.99)	—	—	4(0.27)	6(0.19)	1(0.24)	—	3(0.29)	5(0.22)	9(0.40)	4(27.7)	10(3.49)
Euchaeta media	1(0.35)	—	—	1(0.66)	—	—	1(0.76)	—	—	1(0.04)	1(0.04)	1(6.94)	—
Euchaeta spp. C >2.0 mm	—	—	—	—	—	2(0.01)	—	—	—	—	1(0.08)	—	—
Scolecithricella ≥1.0 mm	3(0.10)	—	—	—	—	1(0)	—	—	1(0)	2(0)	—	—	—
Scottocalanus spp. CV, CVI	—	—	—	—	—	—	—	—	—	1(0.11)	—	—	2(1.54)
Pleuromamma xiphias	10(0.43)	8(0.56)	6(0.77)	2(0.05)	3(0.02)	18(0.07)	—	2(0.12)	10(0.37)	45(0.75)	26(0.45)	10(1.45)	23(1.54)
P. xiphias CV	—	1(0.10)	—	2(0.39)	1(0.06)	6(0.17)	—	1(0.12)	1(0.08)	3(0.11)	—	—	—
P. abdominalis	1(0.16)	2(0.54)	2(0.98)	—	3(0.19)	12(0.35)	1(0.23)	2(0.33)	2(0.21)	9(0.44)	4(0.20)	8(5.56)	12(3.80)
P. abdominalis C	1(0.01)	—	—	—	—	—	—	—	—	—	—	1(0.07)	1(0.02)
P. gracilis	—	—	—	1(0.05)	1(0.02)	3(0.02)	2(0.12)	2(0.03)	2(0.02)	—	1(0)	—	—
Lucicutia spp.	—	—	—	1(0.36)	1(0.12)	—	—	—	—	—	—	—	—
Heterorhabdus papilliger	—	—	—	1(0.20)	—	—	—	—	—	1(0.03)	—	—	—
Candacia longimana	4(0.93)	5(1.89)	1(0.69)	—	3(0.50)	13(0.99)	2(1.19)	2(0.38)	5(0.61)	15(0.82)	2(0.11)	2(2.41)	5(2.74)
Candacia spp. CV, CVI	—	1(0.26)	—	—	1(0.04)	3(0.06)	—	2(0.33)	—	4(0.19)	2(0.10)	—	—
Paracandacia spp. CV, CVI	4(0.18)	—	—	2(0.14)	3(0.06)	5(0.05)	—	1(0.19)	—	3(0.16)	—	—	—
Unident. calanoid	1	—	—	1	2	2	—	1	—	1	—	—	4
Oncaea spp. >0.6 mm	3(0.31)	—	—	6(1.41)	4(0.30)	6(0.21)	1(0.27)	—	8(0.70)	5(0.20)	1(0.04)	3(0.19)	1(0.03)
Corycaeus spp.	—	—	—	—	1(0.04)	1(0.02)	—	—	—	—	—	—	1(0.06)
Euphausia spp.	5(0.04)	6(0.09)	6(0.16)	—	3(0.40)	2(0.12)	—	4(0.64)	5(0.51)	19(0.87)	9(0.42)	—	2(7.14)
Stylocheiron spp.	—	—	—	—	2(0.31)	6(0.45)	—	1(0.49)	3(0.92)	8(1.11)	—	—	7(0.19)
Nematoscelis spp.	—	—	—	—	—	—	—	—	—	—	1(0.38)	—	3(0.07)
Thysanopoda aequalis	—	—	—	—	—	—	1(0.60)	—	—	—	2(1.32)	3(46.9)	2(14.3)
Euphausiid larva	2(0.26)	1(0.21)	1(0.38)	—	1(0.17)	—	—	—	—	3(0.66)	1(0.22)	—	—
Ostracod <1.0 mm	1(0.11)	—	—	—	—	—	—	—	2(0.92)	—	—	—	—
Ostracod 1.0-1.4 mm	—	—	—	—	1(0.02)	3(0.04)	1(0.09)	—	1(0.09)	—	1(0.04)	1(0.05)	1(0.02)
Ostracod 1.5-1.9 mm	—	1(0.10)	—	—	1(0.04)	2(0.03)	1(0.14)	—	—	5(0.33)	—	—	—
Ostracod 2.0-2.9 mm	—	—	—	—	—	1(0.10)	—	—	1(1.22)	—	—	—	—
Amphipod 1.0-1.9 mm	—	1(0.18)	—	—	—	—	—	—	—	—	—	—	—
Amphipod 2.0-2.9 mm	—	—	—	—	—	—	—	—	—	—	1(0.27)	3(1.10)	1(0.17)
Amphipod ≥3.0 mm	1(1.6)	—	—	—	—	—	—	—	—	—	—	—	—
Penaeidean larva	—	1(3.0)	—	—	—	—	—	—	—	—	—	—	1(∞)

Other prey: 70 m: 26-35 mm—2 *Clausocalanus* spp. (0.09), 1 *Neocalanus* spp. (1.2), 1 *Scolecithrix danae* (0.69)
36-45 mm—1 mysid (4.5)
90 m: 36-45 mm—1 *Euaetideus acutus* (0.05)
110 m: 36-45 mm—1 *Thysanopoda* sp. (1.4)
46-50 mm—2 megalopae (5.4), 1 *Undinula darwini* (1.73), 1 cyclopoid (0.09), 1 fish larva (0.31)
170 m: 36-45 mm—1 Penaeidean adult (8.94)
46-54 mm—1 *Nematobrachion sexspinosus* (9.51)

TABLE 5.—Stomach contents of *Lampanyctus nobilis*. Format as in Table 4.

Depth	70 m			90 m		110 m			
Standard length, mm	36-45	47-57	64-78	36-45	46-60	37-45	45-60	62-75	76-86
No. examined	28	11	8	35	30	18	13	23	17
No. with intact prey	19	8	5	22	19	12	10	16	13
No. of intact prey	56	18	9	45	33	32	28	61	25
Prey type	No. (Apparent search volume, m³)								
Aetideidae 2.0-3.0 mm	1(0.19)	—	—	—	1(0.05)	—	—	2(0.12)	—
Aetideidae >3.0 mm	1(0.19)	—	—	2(0.15)	3(0.27)	2(0.31)	1(0.18)	4(0.46)	2(0.28)
Euchaeta media	—	—	1(1.25)	1(0.24)	—	—	1(0.17)	—	—
Pleuromamma xiphias	13(0.53)	3(0.29)	—	2(0.02)	2(0.02)	6(0.35)	10(0.71)	18(0.79)	5(0.27)
P. xiphias CV	—	—	—	1(0.07)	1(0.08)	2(0.25)	1(0.15)	—	—
P. abdominalis	1(0.15)	—	—	6(0.43)	2(0.17)	1(0.17)	—	2(0.25)	—
P. gracilis	3(0.06)	1(0.05)	—	4(0.08)	3(0.07)	2(0.03)	1(0.02)	—	—
Candacia longimana	2(0.47)	5(2.60)	—	1(0.19)	2(0.44)	1(0.19)	3(0.69)	—	—
Candacia spp. CV, CVI	—	—	—	4(0.20)	—	1(0.17)	—	—	—
Paracandacia spp. CV, CVI	1(0.04)	—	—	3(0.07)	2(0.06)	—	—	1(0.14)	—
Oncaea spp. >0.6 mm	2(0.19)	—	—	2(0.17)	—	—	—	—	—
Corycaeus spp.	2(0.04)	—	—	—	1(0.05)	—	—	1(0.04)	—
Euphausia spp.	11(0.09)	5(0.09)	5(0.16)	8(1.21)	4(0.70)	5(0.80)	6(1.15)	12(1.44)	4(0.59)
Stylocheiron spp.	5(0.20)	—	—	2(0.38)	3(0.66)	4(1.95)	4(2.34)	3(1.09)	5(2.25)
Thysanopoda aequalis	2(3.60)	1(4.30)	—	1(0.09)	1(0.22)	3(6.75)	—	5(8.44)	1(2.1)
Thysanopoda spp.	1(5.80)	—	1(22.2)	1(∞)	1(∞)	1(4.9)	—	4(14.7)	2(9.1)

TABLE 5.—*Continued.*

Depth	70 m			90 m		110 m			
Standard length, mm	36-45	47-57	64-78	36-45	46-60	37-45	45-60	62-75	76-86
Prey type	No. (Apparent search volume, m³)								
Euphausiid larva	1(0.12)	—	—	2(0.38)	—	—	—	—	—
Ostracod <1.0 mm	—	—	—	2(0.20)	—	—	—	—	—
Ostracod 1.0-1.4 mm	—	—	—	—	1(0.03)	—	—	—	—
Ostracod 1.5-1.9 mm	—	1(0.14)	1(0.22)	—	1(0.05)	3(0.70)	—	—	—
Ostracod 2.0-2.9 mm	—	—	—	—	—	—	—	—	2(3.60)
Amphipod 1.0-1.9 mm	1(0.11)	—	—	2(0.26)	—	—	—	—	1(0.60)
Amphipod 2.0-2.9 mm	5(1.75)	1(0.83)	—	—	—	—	—	—	—
Amphipod ≥3.0 mm	—	—	—	—	2(3.00)	—	—	2(1.76)	2(2.20)
Penaeidean juvenile + adult	—	—	—	—	—	1(3.5)	1(4.2)	4(10.4)	—

Other prey: 70 m: 36-45 mm—1 *Neocalanus* spp. (1.14). 1 *Scolecithrix danae* (0.65), 1 *Scottocalanus* spp. (0.25), 1 *Lucicutia* spp. (0.07)
47-57 mm—1 *Nannocalanus minor* (0.12)
64-78 mm—1 mysid (10.09)
90 m: 36-45 mm—1 *Eucalanus* spp. (2.30)
46-60 mm—1 *Heterorhabdus* spp. (≠), 1 Aetideidae C ≤2.0 mm (0.05), 1 megalopa (1.05)
110 m: 62-75 mm—1 *Euchaeta* spp. (1.6), 1 *Pleuromamma abdominalis* C (0.09), 1 *Nematoscelis* spp (0.96)
76-86 mm—1 Caridean juvenile (19.2)

TABLE 6.—Stomach contents of *Triphotorus nigrescens* and *Notolychnus valdiviae*. Format as in Table 4.

Species	*T. nigrescens*			*N. valdiviae*	
Depth	70 m		90 m	110 m	170 m
Standard length, mm	19-25	26-37	16-24	19-24	20-23
No. examined	32	29	59	77	88
No. with intact prey	30	28	28	62	55
No. of intact prey	108	99	52	138	92
Prey type	No. (Apparent search volume, m³)				
Calanus tenuicornis	—	—	1(0.01)	2(0.01)	1(0.03)
Nannocalanus minor	2(0.07)	1(0.04)	—	—	—
Undinula vulgaris	2(0.83)	1(0.45)	—	—	—
Undinula darwini	1(0.28)	1(0.30)	—	—	—
Clausocalanus spp.	—	—	—	1(0.01)	1(0.04)
Gaetanus spp.	—	—	1(0.10)	—	4(0.42)
Aetideidae C <2.0 mm	—	—	2(0.07)	2(0.03)	4(0.29)
Aetideidae C 2.0-3.0 mm	2(0.24)	1(0.13)	1(0.04)	—	10(0.83)
Aetideidae CV, CVI >3.0 mm	2(0.24)	2(0.26)	1(0.06)	2(0.06)	2(0.44)
Euchaeta media	1(0.21)	2(0.45)	1(0.19)	1(0.03)	1(2.00)
Scolecithrix danae	1(0.42)	1(0.45)	—	—	—
Scolecithricella spp. <1.0 mm	2(0.15)	2(0.16)	—	—	—
Scolecithricella spp. ≥1.0 mm	1(0.02)	2(0.04)	—	1(0)	2(0.03)
Scottocalanus spp. CV, CVI	—	1(0.17)	—	—	1(0.49)
Pleuromamma xiphias	14(0.36)	25(0.69)	3(0.02)	14(0.16)	25(1.10)
P. xiphias CV	—	1(0.04)	—	4(0.10)	4(0.09)
P. abdominalis	5(0.49)	3(0.31)	1(0.06)	9(0.30)	1(0.20)
P. abdominalis C	—	2(0.02)	—	—	2(0.20)
P. gracilis	6(0.08)	6(0.08)	2(0.03)	2(0.01)	—
Lucicutia spp.	—	1(0.05)	1(0.10)	1(0.05)	1(0.02)
Heterorhabdus spp.	—	—	—	2(0.40)	1(0.13)
Candacia longimana	3(0.42)	5(0.74)	5(0.74)	3(0.11)	5(1.75)
Candacia spp. CV, CVI	—	—	1(0.04)	1(0.03)	—
Paracandacia spp. CV, CVI	2(0.05)	4(0.12)	—	3(0.11)	2(≠)
Unident. calanoid	—	1	1	2	3
Oncaea spp. >0.6 mm	43(2.65)	12(0.79)	22(1.48)	74(1.99)	21(0.38)
Corycaeus spp.	2(0.02)	1(0.01)	—	—	—
Euphausia spp.	4(0.02)	12(0.07)	—	1(0.03)	—
Euphausiid larva	3(0.23)	2(0.16)	—	3(0.45)	—
Ostracod <1.0 mm	3(0.20)	—	4(0.31)	2(0.28)	—
Ostracod 1.0-1.4 mm	—	1(0.02)	3(0.06)	—	—
Ostracod 1.5-1.9 mm	1(0.04)	1(0.04)	1(0.03)	1(0.10)	—
Amphipod 1.0-1.9 mm	2(0.14)	1(0.07)	1(0.10)	—	—
Amphipod 2.0-2.9 mm	3(0.67)	1(0.24)	—	—	—
Amphipod ≥3.0 mm	2(2.22)	1(1.19)	—	3(0.23)	—

Other prey:
T. nigrescens— 70 m: 19-25 mm —1 *Neocalanus* spp. (0.72)
26-37 mm —1 megalopa (1.38), 1 *Stylocheiron* spp. (0.14) 1 *Euaetideus acutus* (0.08), 2 *Euchaeta* spp. C >2.0 mm (0.42)
N. valdiviae —110 m: 19-25 mm —1 *Scolecithrix bradyi* (0.02), 1 *Pleuromamma gracilis* CV (0.02), 1 *Heterorhabdus papilliger* (0.02), 1 *Stylocheiron* spp. (0.09)
—170 m: 20-23 mm —1 zoea (≠)

small to medium copepods and euphausiids, the latter of which were taken frequently.

Notolychnus valdiviae (Table 6)

Notolychnus valdiviae occurs throughout the depth range covered by the three deepest samples as evidenced by the high numbers of specimens available from each depth. With such large catches, it is unlikely that data from the deeper samples were seriously affected by catches in transit to and from towing depth.

Microzooplankton made up over half the diet at 90 and 110 m and about one-fourth at 170 m (Table 2). These were almost all *Oncaea*. If the ASV's are roughly corrected for undersampling, they are still relatively high at 90 and 110 m.

Most of the remaining prey were medium to large copepods; *P. xiphias*, *P. abdominalis*, *C. longimana*, and aetideids were important at one or more depths. Euphausiids were rarely taken. ASV's for items from 90 and 110 m were mostly rather low (Table 2). At 170 m ASV's for a large fraction of items and prey types were high (> 0.80 m^3) mainly due to high values for *P. xiphias*, *C. longimana*, and 2-3 mm aetideids. This plus the lower proportion of microzooplankton in the diet at 170 m indicates increased preference for larger prey.

Ceratoscopelus warmingi (Table 7)

Ceratoscopelus warmingi took a wide variety of sizes and taxa of prey. Small fractions of the diets of the large fish were microzooplankton—mostly *Oncaea* spp., but including several species of small calanoids, ostracods, and gastropod veligers. *Oncaea* and small ostracods made up over a third of the diet of the small fish from 90 m (Table 2). If the ASV's for *Oncaea* are decreased by a factor of 4 to roughly correct for undersampling, preference equivalent to that for larger prey is indicated. ASV's for other microzooplankton were very low. All sizes of calanoids and small to medium ostracods were taken, but ASV's were usually low.

Many prey items were large and most of these had high ASV's, resulting in large fractions of the prey from large fish at 70 and 110 m having high ASV's (Table 2). Euphausiids, decapods and their larvae, large amphipods, and ostracods were taken frequently, but fish, siphonophores, heteropods, and polychaetes (all >5 mm) were also present. Items listed as "fish" (Table 7) were all epipelagic larvae or juveniles, but *C. warmingi* also frequently eats *Cyclothone*, which it encounters only during the day. Results of studies of feeding chronology (Clarke 1978) indicate that *Ceratoscopelus warmingi* takes such large items both day and night. While it is possible that the other large items mentioned above could have been taken at depths other than those sampled and thus that the high ASV's are artifacts, these items do cooccur with *C. warmingi* at the depths sampled and those recorded were relatively fresh and intact in stomachs of fish collected in the latter half of the night. (*Cyclothone* were, however, eliminated for calculations in Table 2.) Even allowing for the probability that ASV's of some of the largest prey types were overestimated due to avoidance of the plankton nets (see Methods sec-

TABLE 7.—Stomach contents of *Ceratoscopelus warmingi*. Format as in Table 4.

Depth	70 m	90 m		110 m
Standard length, mm	46-69	38-45	46-62	46-68
No. examined	23	16	90	25
No. with intact prey	12	12	61	14
No. of intact prey	57	34	179	55
Prey type	No. (Apparent search volume, m^3)			
Nannocalanus minor	1(0.08)	1(0.18)	—	—
Aetideidae C 2.0-3.0 mm	1(0.30)	—	1(0.02)	—
Aetideidae CV, CVI >3.0 mm	1(0.30)	2(0.28)	3(0.08)	2(0.26)
Pleuromamma xiphias	2(0.13)	3(0.05)	9(0.03)	2(0.10)
P. abdominalis	—	2(0.27)	6(0.16)	3(0.43)
P. abdominalis C	1(0.02)	1(0.22)	1(0.04)	—
P. gracilis	2(0.06)	2(0.07)	1(0.01)	—
Lucicutia spp.	1(0.11)	—	4(0.09)	1(0.23)
Paracandacia spp. CV, CVI	—	—	1(0.01)	1(0.16)
Unident. calanoid	—	2	—	2
Oncaea spp. >0.6 mm	7(1.08)	10(1.57)	20(0.62)	4(0.48)
Corycaeus spp.	—	1(0.07)	2(0.03)	
Euphausia spp.	6(0.08)	3(0.83)	8(0.44)	7(0.96)
Stylocheiron spp.	—	—	4(0.27)	7(2.90)
Thysanopoda aequalis	3(8.60)	2(0.69)	6(0.41)	6(11.6)
Euphausiid larva	3(0.58)	1(0.35)	3(0.20)	2(1.3)
Ostracod <1.0 mm	3(0.09)	2(0.36)	3(0.11)	—
Ostracod 1.0-1.4 mm	1(0.06)	—	12(0.12)	2(0.24)
Ostracod 1.5-1.9 mm	2(0.18)	1(0.08)	9(0.72)	—
Ostracod ≥2.0 mm	5(4.50)	—	5(0.34)	3(4.30)
Amphipod 1.0-1.9 mm	—	—	5(0.05)	—
Amphipod 2.0-2.9 mm	—	—	3(0.53)	—
Amphipod ≥3.0 mm	6(14.2)	1(2.40)	4(1.90)	—
Penaeidean juvenile + adult	—	—	1(0.55)	2(5.90)
Mysid	1(4.20)	—	—	2(20.4)
Polychaete	—	—	1(0.08)	2(1.70)
Siphonophore	1(0.12)	—	5(0.06)	—
Fish larva	2(0.79)	—	8(0.94)	4(3.60)
Cyclothone spp.	1(∞)	—	26(∞)	—

Other prey:

70 m—1 *Undinula darwini* (0.69), 1 *Heterorhabdus papilliger* (0.10), —1 Augaptilidae (0.52), 1 megalopa (3.20), 2 stomatopod larvae —(∞), 1 Ctenophore (∞).

90 m—46-62 mm—1 *Calanus tenuicornis* (0.01), 2 *Clausocalanus* spp. (0.03), 1 Pseudocalanidae (0.55), 1 *Ischnocalanus* sp. (∞), 1 Aetideidae C <2.0 mm (0.02), 1 *Euchaeta media* (0.09), 1 *Scolecithrix bradyi* (0.04), 2 *Candacia longimana* (0.14), 5 *Candacia* spp. CV, CVI (0.09), 1 Caridean larva (0.23), 1 Penaeidean larva (0.33), 2 Anomuran larvae (∞), 1 Chaetognath (0), 6 Heteropods (1.14), 2 Gastropods (0.16).

110 m—2 *Nematoscelis* spp. (2.20), 1 *Nematobrachion sexspinosus* (23.8).

tion), the high ASV's observed probably indicate a real preference for large prey.

A 48 mm *Ceratoscopelus warmingi* female from 90 m had no lenses in the eyes. The outer eye cover was intact and the space normally occupied by the lens was filled with gelatinous material similar to the humor in the rest of the eye. Thus the lenses were not missing due to damage during capture or even a recent injury. This fish had not only managed to reach adult size, but had three fresh copepods and remains of others and a euphausiid in the stomach.

Bolinichthys longipes (Table 8)

Trematode parasites were frequently present in the stomachs of *B. longipes*. The large fish from 110 m averaged over six parasites/stomach (Table 8). Parasite load and frequency was much lower in the small fish from 70 m. It was not possible, due to insufficient numbers, to rigorously compare stomach contents of fish with and without parasites from any given depth-size group; however, while some of the unparasitized fish had more intact prey than most parasitized specimens, there were no obvious differences in prey type or frequency. Thus the parasites did not appear to bias the diet directly or by effectively increasing digestion rate and causing more resistant prey types to appear as intact in disproportionate frequencies.

Microzooplankton, 90% of which were *Oncaea* spp., made up the great majority of food items in all groups (Table 2). A large fraction of the *Oncaea* spp. eaten were very small (≤0.6 mm); such sizes were rarely eaten by most of the other fishes considered. The ASV's for these small forms were absurdly high; data from very fine mesh plankton nets would be needed to estimate preference. If the ASV's for the large *Oncaea* are reduced by a factor of 4 (see Methods section), the values are still quite

TABLE 8.—Stomach contents of *Bolinichthys longipes* and *Diogenichthys atlanticus*. Format as in Table 4. Also given are incidence and number per fish of trematode parasites in *B. longipes*.

Species	*B. longipes*					*D. atlanticus*
Depth	70 m	90 m		110 m		70 m
Standard length, mm	17-26	27-35	36-47	26-35	36-49	17-21
No. examined	11	25	35	38	35	9
No. with intact prey	11	25	35	38	35	6
No. of intact prey	78	127	168	238	323	43
No. with trematodes	3	19	35	36	32	—
Average (range) no./fish	0.36(0-2)	1.84(0-6)	3.48(1-9)	2.74(0-8)	6.03(0-12)	—
Prey type	No. (Apparent search volume, m³)					
Calanus tenuiformis	—	2(0.03)	1(0.01)	—	1(0.01)	—
Acrocalanus spp.	—	—	—	—	—	3(5.40)
Clausocalanus spp.	1(0.07)	—	—	—	1(0.01)	—
Euaetideus acutus	—	1(0.10)	2(0.15)	—	2(0.06)	—
Aetideidae CV, CVI >3.0 mm	1(0.33)	1(0.07)	1(0.05)	—	1(0.05)	—
Scolecithrix bradyi	1(0.12)	2(0.21)	2(0.15)	2(0.06)	4(0.14)	2(0.45)
Scolecithricella spp. <1.0 mm	—	1(0.12)	1(0.09)	—	—	—
Scolecithricella spp. ≥1.0 mm	—	—	—	1(0)	—	1(0.10)
Pleuromamma xiphias	1(0.07)	1(0.01)	2(0.01)	4(0.07)	10(0.20)	—
P. abdominalis	—	1(0.06)	—	2(0.11)	2(0.11)	—
P. gracilis	—	2(0.03)	1(0.01)	4(0.02)	2(0.01)	1(0.06)
Lucicutia spp.	—	—	1(0.08)	1(0.08)	—	2(0.45)
Heterorhabdus papilliger	—	—	1(0.05)	1(0.03)	—	—
Candacia longimana	1(0.38)	1(0.17)	2(0.24)	2(0.12)	10(0.66)	—
Candacia spp CV, CVI	—	1(0.04)	2(0.06)	8(0.41)	26(1.46)	—
Paracandacia spp. CV, CVI	1(0.07)	2(0.04)	5(0.15)	1(0.06)	15(0.97)	1(0.14)
Unident. calanoid	1	2	2	2	6	3
Oithona spp.	—	1(0.05)	1(0.04)	—	—	—
Oncaea spp. >0.6 mm	17(2.86)	45(3.40)	86(4.64)	125(5.48)	150(7.14)	11(3.40)
Oncaea spp. ≤0.6 mm	42(95)	52(∞)	42(∞)	78(205)	84(240)	11(45.8)
Corycaeus spp.	1(0.03)	2(0.07)	1(0.03)	—	2(0.04)	—
Microsetella spp.	2(∞)	1(∞)	1(∞)	2(∞)	—	4(∞)
Euphausia spp.	—	—	—	—	1(0.05)	1(0.03)
Euphausiid larva	2(0.42)	—	—	—	1(0.27)	—
Ostracod <1.0 mm	1(0.18)	5(0.44)	3(0.19)	—	2(0.50)	—
Ostracod 1.0-1.4 mm	—	—	2(0.03)	2(0.09)	1(0.05)	—
Ostracod 1.5-1.9 mm	3(0.31)	—	2(0.05)	1(0.07)	1(0.08)	1(0.18)
Amphipod 1.0-1.9 mm	1(0.18)	1(0.11)	1(0.08)	—	—	1(0.33)
Chaetognath	—	—	—	1(0.02)	—	1(0.05)
Gastropod larva	1(0.03)	—	1(0.14)	—	—	—

Other prey: *B. longipes* — 70 m: 17-26 mm—1 *Pontella* sp. (∞)
90 m: 26-35 mm—2 Aetideidae C <2.0 mm (0.08), 1 *Euchaeta media* (0.21)
36-47 mm—2 *Lophothrix* spp. (0.14), 1 *Gaetanus* sp. (0.08), 1 *Pareuchaeta* sp. (∞), 1 zoea (9.50)
110 m: 26-35—1 Amphipod <1.0 mm (∞)
36-49—1 *Stylocheiron* sp. (0.17)

high, indicating a real preference for *Oncaea*. Except for three prey types not taken by the plankton tows, the ASV's for other microzooplankton are low even without any adjustment for undersampling.

Except for the large fish from 110 m, macrozooplankton were taken very infrequently and mostly had low ASV's. The large fish from 110 m had eaten *Pleuromamma* and candaciids frequently, and this was the only group from which euphausiids were recorded. The data indicate some preference for candaciids. ASV's for these copepods were high for the large fish from 110 m and sometimes fairly high in other groups.

Diogenichthys atlanticus (Table 8)

About three-fourths of the items eaten by *D. atlanticus* were microzooplankton—mostly *Oncaea* spp. The ASV for the grossly undersampled small *Oncaea* is meaningless, but if ASV's for the other microzooplankton are reduced by a factor of 4, there is reasonable indication of preference for the large *Oncaea* spp. and *Acrocalanus* spp. Most of the macrozooplankton were small to medium copepods, and ASV's of most types were low.

Benthosema suborbitale (Table 9)

Benthosema suborbitale usually does not occur as deep as 110 m, but the number collected at that depth was considerably larger than that expected from catches in transit. Thus the data are probably not seriously affected by fish caught at shallower depths. The sample from 90 m, which was taken at a different time of the year, had too few *B. suborbitale* to merit analysis.

Microzooplankton were important fractions of the diet of *B. suborbitale*; they made up over half the items from the small fish and slightly less for the larger ones. Almost all were *Oncaea* spp.—mostly the larger forms. Macrozooplankton were mostly medium to large copepods, but also included euphausiids and large amphipods. Such prey, especially *P. xiphias* and candaciids, were eaten more frequently by the large fish from both depths. ASV's for most macrozooplankton prey types were 0.40 m^3 or less. If the ASV's for the large *Oncaea* spp. are reduced by a factor of 4, they are commensurate with those of the macrozooplankton.

TABLE 9.—Stomach contents of *Benthosema suborbitale*. Format as in Table 4.

Depth	70 m		110 m
Standard length, mm	18-25	26-30	26-32
No. examined	20	48	38
No. with intact prey	11	32	26
No. of intact prey	29	69	47
Prey type	No. (Apparent search volume, m^3)		
Nannocalanus minor	—	—	1(0.98)
Undinula darwini	1(0.75)	2(0.52)	—
Clausocalanus spp.	1(0.07)	—	1(0.02)
Aetideidae C 2.0-3.0 mm	—	—	3(0.12)
Aetideidae CV, CVI >3.0 mm	1(0.33)	1(0.11)	2(0.14)
Euchaeta media	—	1(0.20)	—
Scolecithrix danae	1(1.14)	—	—
Pleuromamma xiphias	1(0.07)	11(0.27)	8(0.22)
P. xiphias CV	1(0.10)	1(0.03)	—
P. abdominalis	1(0.27)	2(0.18)	2(0.15)
P. gracilis	1(0.04)	2(0.02)	3(0.02)
Heterorhabdus papilliger	1(0.11)	—	—
Candacia longimana	1(0.38)	3(0.39)	—
Candacia spp. CV, CVI	—	1(0.09)	1(0.08)
Paracandacia spp. CV, CVI	—	5(0.13)	3(0.26)
Unident. calanoid	1	—	—
Oncaea spp. >0.6 mm	10(1.68)	21(1.22)	19(1.22)
Oncaea spp. ≤0.6 mm	4(9.09)	8(6.25)	1(3.85)
Corycaeus spp.	—	2(0.02)	1(0.03)
Euphausia spp.	—	3(0.01)	1(0.07)
Thysanopoda aequalis	—	2(2.20)	—
Euphausiid larva	3(0.63)	1(0.07)	—
Ostracod 1.5-1.9 mm	1(0.10)	1(0.03)	—
Amphipod 1.0-1.9 mm	—	1(0.06)	—
Amphipod 2.0-2.9 mm	—	—	1(0.42)
Zoea	—	1(0.04)	—

Diaphus schmidti (Table 10)

The numbers of prey per fish and diversity of prey were relatively high for *D. schmidti*; several small copepods and noncrustacean prey that were either rare or absent in the diets of other species were taken relatively frequently.

Microzooplankton made up 30-50% of the items (Table 2); half to two-thirds of these were *Oncaea*. If ASV's for *Oncaea* are roughly corrected, they are still quite high. ASV's for other types of microzooplankton were variable.

Although the composition of macrozooplankton prey was generally similar for all groups, there were some differences between sizes or depths. *Pleuromamma* and *Euphausia* spp. were eaten more frequently at 70 m than at 90 m. Overall, *Corycaeus* spp. were the most frequently eaten prey, but at both depths, frequency and ASV's were higher for the small fish. About half the prey of the small fish from 70 m had high ASV's. These were mostly *Corycaeus* spp., but also included several medium to large prey types. Among the large fish from 70 m, a few types of large prey had high ASV's, but most prey from both these and both groups from 90 m had low ASV's. The generally higher ASV's associated with the small fish from 70 m appear to have resulted mostly from higher

TABLE 10.—Stomach contents of four *Diaphus* species. Format as in Table 4.

Species	*D. schmidti*				*D. perspicillatus*	*D. fragilis*	*D. trachops*
Depth	70 m		90 m		70 m	90 m	170 m
Standard length, mm	31-35	36-40	27-35	36-41	46-56	34-44	36-50
No. examined	12	15	30	21	20	6	15
No. with intact items	11	14	30	19	17	5	12
No. of intact items	162	124	188	81	457	29	32
Prey type	No. (Apparent search volume, m³)						
Neocalanus spp.	2(3.90)	—	—	—	2(2.60)	—	—
Calanus tenuicornis	—	—	2(0.03)	—	—	1(0.08)	—
Nannocalanus minor	2(0.18)	2(0.14)	3(0.22)	—	8(0.48)	—	—
Undinula vulgaris	1(1.10)	1(0.89)	—	—	6(0.44)	—	—
U. darwini	5(3.80)	2(1.20)	1(0.09)	—	4(2.00)	—	—
Acrocalanus spp.	—	1(0.76)	1(×)	—	2(1.30)	1(×)	—
Clausocalanus spp.	1(0.07)	—	2(0.06)	1(0.05)	—	—	—
Gaetanus + *Chiridius* spp.	—	—	—	1(0.15)	—	—	7(3.30)
Aetideidae C <2.0 mm	—	—	—	—	—	1(0.21)	4(1.30)
Aetideidae C 2.0-3.0 mm	—	—	3(0.10)	—	—	1(0.21)	1(0.38)
Aetideidae CV, CVI >3.0 mm	—	1(0.26)	—	1(0.09)	9(1.90)	—	2(2.00)
Euchaeta media	1(0.57)	—	—	—	5(1.80)	—	—
Scolecithrix danae	2(2.30)	1(0.89)	—	—	—	—	—
Scottocalanus spp. CV, CVI	—	—	—	—	1(2.80)	—	2(4.50)
Pleuromamma xiphias	2(0.14)	6(0.33)	4(0.03)	5(0.05)	29(1.30)	5(0.20)	1(0.19)
P. xiphias CV	2(0.20)	—	—	—	1(0.06)	—	—
P. abdominalis	6(1.60)	7(1.50)	2(0.11)	3(0.25)	23(4.00)	1(0.32)	1(0.93)
P. abdominalis C	—	1(0.02)	—	1(0.14)	3(0.05)	—	—
P. gracilis	10(0.35)	4(0.14)	3(0.04)	3(0.07)	51(1.16)	1(0.08)	—
Centropages spp.	—	—	1(1.70)	—	2(1.40)	—	—
Lucicutia spp.	4(0.49)	5(0.48)	5(0.48)	1(0.15)	18(1.40)	—	2(0.17)
Heterorhabdus papilliger	1(0.11)	1(0.09)	—	—	—	—	1(0.47)
Candacia longimana	—	1(0.30)	1(0.14)	—	5(1.20)	1(0.83)	—
Candacia spp. CV, CVI	—	1(0.21)	3(0.11)	2(0.11)	1(0.17)	—	—
Paracandacia spp. CV, CVI	2(0.15)	2(0.11)	1(0.06)	2(0.06)	20(0.96)	1(0.11)	—
Acartia spp.	1(0.24)	1(0.19)	1(0.15)	—	2(0.31)	1(0.90)	—
Unident. calanoid	8	4	8	3	38	—	3
Oithona spp.	—	—	1(0.04)	—	1(0.07)	—	—
Oncaea spp. >0.6 mm	32(5.39)	35(4.63)	46(2.89)	24(2.38)	121(13.20)	9(3.39)	2(0.17)
Corycaeus spp.	40(1.25)	16(0.39)	23(0.69)	6(0.28)	34(0.69)	—	2(0.34)
Other cyclopoids	1(0.61)	2(0.95)	1(0.04)	—	2(0.78)	—	—
Euphausia spp.	7(0.10)	5(0.06)	4(0.44)	1(0.17)	13(0.12)	—	—
Stylocheiron spp.	2(0.69)	1(0.27)	—	1(0.22)	4(0.09)	—	—
Thysanopoda aequalis	—	—	—	1(0.22)	—	—	1(20.80)
Euphausiid larva	2(0.42)	—	11(1.50)	3(0.66)	6(0.81)	—	—
Ostracod <1.0 mm	5(0.91)	4(0.57)	10(0.72)	3(0.34)	2(0.24)	4(1.70)	1(0.22)
Ostracod 1.0-1.4 mm	5(0.33)	2(0.10)	3(0.06)	1(0.03)	6(0.25)	1(0.12)	—
Ostracod 1.5-1.9 mm	2(0.20)	3(0.24)	7(0.22)	6(0.31)	4(0.26)	—	—
Amphipod 1.0-1.9 mm	—	1(0.14)	1(0.09)	1(0.15)	—	—	—
Amphipod 2.0-2.9 mm	—	2(0.95)	3(1.07)	—	—	—	—
Amphipod ≥3.0 mm	—	1(2.0)	—	—	1(1.70)	—	—
Caridean larva	1(0.18)	2(0.29)	—	1(0.75)	16(1.90)	—	—
Penaeidean larva	—	—	1(0.67)	—	—	1(4.00)	—
Zoea	—	—	1(11.1)	—	—	—	1(×)
Megalopa	3(10.50)	—	1(0.67)	—	1(2.30)	—	—
Chaetognath	—	—	2(0.02)	—	2(0.04)	—	
Larvacean	2(1.30)	1(0.52)	—	—	—	—	—
Gastropod larva	4(0.13)	3(0.08)	11(1.70)	1(0.25)	3(0.06)	—	—
Pelecypod larva	3(2.30)	—	14(20.30)	6(13.70)	2(0.98)	—	—

Other prey: *D. schmidti*—70 m: 31-35 mm—1 *Eucalanus* sp. (1.60), 2 isopods (×)
36-40 mm—1 *Neocalanus* CV (0.11), 1 Unident. Harpactacoid (×), 1 *Thysanopoda* sp. (7.90), 2 pteropods >1.0 mm (×)
90 m: 27-35 mm—1 *Scolecithrix bradyi* (0.09), 1 *Calocalanus* sp. (×), 2 heteropods (0.95), 1 Penaeidean juvenile/adult (1.10), 1 polychaete (0.17), 1 fish larva (0.24)
36-41 mm—1 *Ischnocalanus* sp. (×), 1 amphipod <1.0 mm (×), 1 ostracod >3.0 mm (1.10)
D. perspicillatus—3 *Euchaeta rimana* (×), 1 *Euchaeta* sp. (0.63), 1 *Scolecithricella* sp. <1.0 mm (0.13), 1 *Nematoscelis* sp. (2.70), 1 Caridean juvenile/adult (0.84), 1 polychaete larva (×), 1 insect (×)
D. trachops—1 Siphonophore (11.90)

numbers of prey per fish rather than from any obvious differences in diet composition or relative preference.

Diaphus perspicillatus (Table 10)

The number of prey per fish for *D. perspicillatus* was the highest of any species included and, possibly because of this, so was the diversity of prey. Almost a third of the prey were microzooplankton (Table 2)—the great majority of these, *Oncaea* spp. The ASV for *Oncaea*, if corrected, is still high, as were the ASV's for about half the macrozooplankton prey types. The most frequent macrozooplankton were small copepods: *P. gracilis*, *Lucicutia*, *Paracandacia*; but several medium to

large prey: *Pleuromamma xiphias*, *P. abdominalis*, and large aetideids, were eaten frequently. Several small to medium copepods, the most frequent of which was *Corycaeus*, had intermediate ASV's (0.41-0.70 m^3). Very few prey had low ASV's; half of these were ostracods and euphausiids.

Diaphus fragilis (Table 10)

Few *D. fragilis* were available, and number of prey items was low. The data are most similar to those for *D. schmidti*. Microzooplankton accounted for about one-half the diet. The corrected ASV for *Oncaea* spp., the dominant microzooplankton, and those of most macrozooplankton were low. Only two prey types—each taken only once—had ASV's over 0.40 m^3.

Diaphus trachops (Table 10)

Data for *D. trachops* are few, but indicate that its diet is quite different from those of the other *Diaphus* spp. in that few microzooplankton were eaten. Most prey items were medium to large forms and had high ASV's.

TABLE 11.—Stomach contents of *Melamphaes danae* and *Bregmaceros japonicus*. Format as in Table 4.

Species	*M. danae*			*B. japonicus*
Depth	70 m	90 m	110 m	70 m
Standard length, mm	17-22	19-22	19-22	38-51
No. examined	26	15	10	23
No. with intact prey	18	10	8	18
No. of intact prey	54	32	34	41
Prey type	No. (Apparent search volume, m^3)			
Neocalanus spp.	3(3.60)	—	1(0.96)	—
Calanus tenuicornis	—	—	1(0.05)	—
Nannocalanus minor	2(0.11)	—	3(9.60)	1(0.06)
Undinula darwini	1(0.46)	—	1(8.90)	—
Clausocalanus spp.	—	—	1(0.05)	—
Aetideidae C 2.0-3.0 mm	—	1(0.10)	—	—
Aetideidae CV, CVI > 3.0 mm	1(0.20)	—	1(0.23)	—
Euchaeta rimana	3(×)	—	2(×)	1(×)
Scolecithricella spp. <1.0 mm	—	1(0.31)	—	—
Pleuromamma xiphias	—	—	—	12(0.52)
P. xiphias CV	—	—	—	2(0.12)
P. abdominalis	—	—	—	5(0.82)
P. gracilis	—	—	—	1(0.02)
Heterorhabdus papilliger	—	—	—	1(0.07)
Candacia longimana	—	—	—	2(0.46)
Paracandacia spp.	1(0.04)	—	1(0.29)	—
Unident. calanoid	—	1	—	—
Oncaea spp. >0.6 mm	—	1(0.19)	—	—
Oncaea spp. ≤0.6 mm	—	—	—	1(1.38)
Corycaeus spp.	4(0.07)	5(0.45)	2(0.18)	—
Euphausia spp.	1(0.01)	—	1(0.24)	2(0.02)
Euphausiid larva	4(0.51)	4(1.67)	6(6.95)	4(0.51)
Ostracod <1.0 mm	4(0.44)	3(0.65)	1(1.10)	—
Ostracod 1.0-1.4 mm	2(0.08)	5(0.30)	—	—
Ostracod 1.5-1.9 mm	2(0.12)	2(0.19)	—	—
Amphipod 1.0-1.9 mm	5(0.57)	—	—	—
Amphipod 2.0-2.9 mm	5(1.85)	—	2(2.70)	—
Caridean larva	1(0.11)	—	2(3.20)	4(0.44)
Penaeidean larva	1(1.80)	—	—	—
Mysid	—	—	1(17.90)	—
Chaetognath	6(0.11)	6(0.18)	7(0.81)	5(0.09)
Heteropod	—	1(1.43)	—	—
Gastropod larva	8(0.16)	2(0.95)	1(0.72)	—

Melamphaes danae (Table 11)

Microzooplankton made up minor fractions of the diet of *M. danae*; most were either small ostracods or gastropods. Among the other prey only chaetognaths and euphausiid larvae were consistently important. At 70 and 90 m, 22 and 26% of the prey had high ASV's; most other types had low values (Table 2). At 110 m, the great majority of prey types and items had high ASV's. For most prey types, the ASV's at different depths were either consistently high (euphausiid larvae, *Neocalanus*, amphipods) or low (ostracods), but the value for chaetognaths at 110 m was much higher than shallower.

Bregmaceros japonicus (Table 11)

Bregmaceros japonicus ate few microzooplankton; small macrozooplankton were also taken infrequently and usually with low ASV. Most prey were medium to large and, except for chaetognaths and *Euphausia* spp., ASV's were moderate to high.

DISCUSSION

The fishes considered here clearly showed preference in a broad sense, i.e., some abundant zooplankton were rarely or never taken, and the ASV's of types regularly eaten were variable. Though there were exceptions, these fishes generally grazed on relatively large, visible crustaceans. Other taxa were rarely taken and then usually with low ASV's. Most other taxa in the plankton were either translucent forms, e.g., chaetognaths and tunicates, or quite small, e.g., gastropod veligers. Among the crustacean microzooplankton, the densely pigmented and relatively opaque *Oncaea* spp. were the only types that were taken regularly and had high ASV's. Some apparently less visible forms such as *Clausocalanus* and small *Scolecithricella* spp. were abundant in the plankton samples (in spite of mesh escapement), but rarely eaten, and the undoubtedly more numerous smaller types which mostly passed through the plankton net mesh were absent from almost all the fishes' diets. Among the crustacean macrozooplankton, several translucent or weakly

pigmented types, e.g., *Calanus tenuicornis* and *Neocalanus* and *Pleuromamma* spp. copepodites, were abundant but mostly ignored by the fishes.

Difference between species' diets were often correlated with differences in one or more of the morphological features examined (Figures 1-4). The

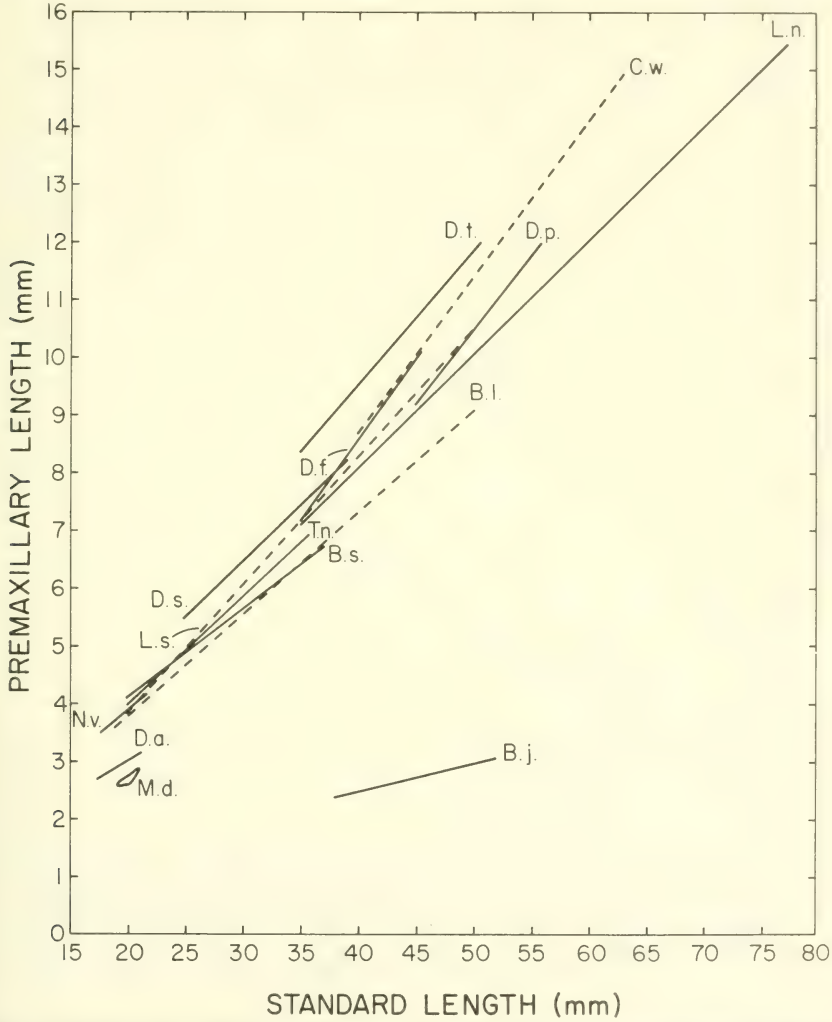


FIGURE 1.—Relationships between standard length and premaxillary length for 14 species of mesopelagic fishes designated by initials of genus and species names. Lines for *Lampanyctus nobilis*, *Triphoturus nigrescens*, *Notolychnus valdiviae*, *Benthosema suborbitale*, *Diogenichthys atlanticus*, *Diaphus schmidti*, *D. perspicillatus*, *D. fragilis*, *D. trachops*, and *Bregmaceros japonicus* and (dashed lines) for *Lampanyctus steinbecki*, *Ceratoscopelus warmingi*, and *Bolinichthys longipes* are drawn from equations determined by least squares regression on measurements from five or more specimens of each species over the size ranges plotted; coefficients of determination (r^2) exceeded 0.80 for all. *Melamphaes danae* ($r^2 = 0.48$) is represented by the area enclosed by points from five specimens.

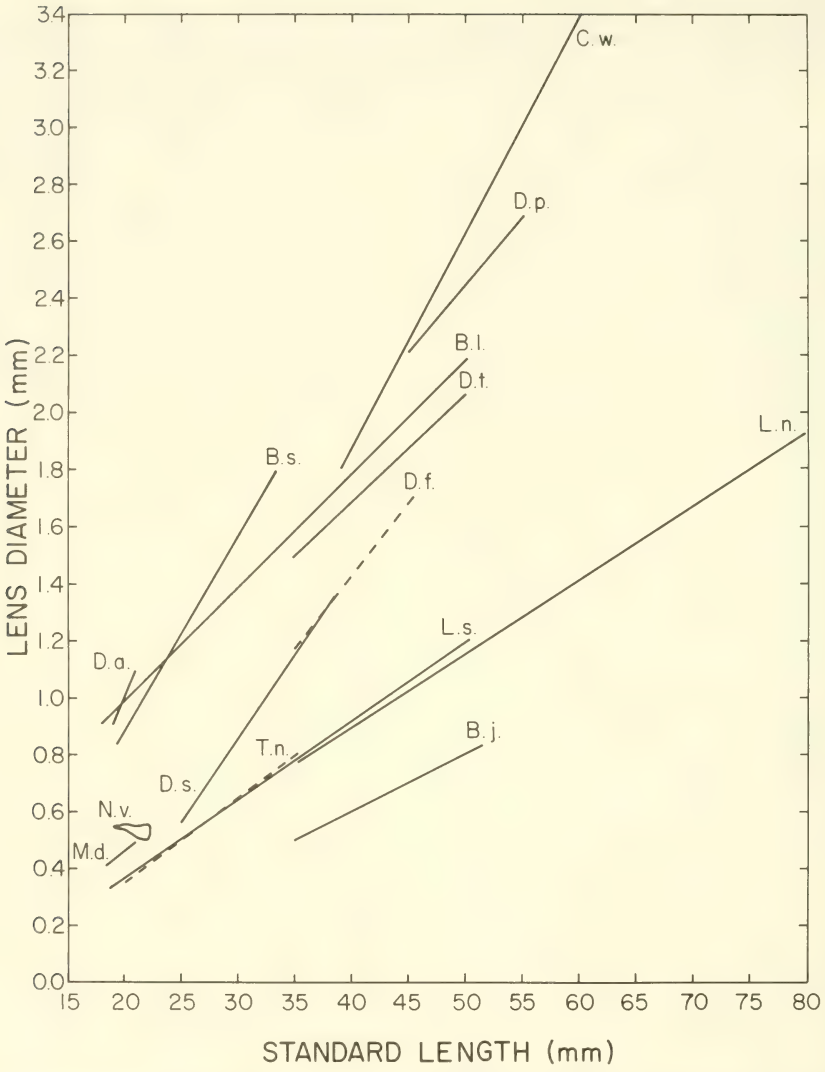


FIGURE 2.—Relationships between standard length and lens diameter for 14 species of mesopelagic fishes designated by initials of genus and species names. Lines for *Lampanyctus steinbecki*, *L. nobilis*, *Ceratoscopelus warmingi*, *Benthosema suborbitale*, *Diogenichthys atlanticus*, *Bolinichthys longipes*, *Diaphus schmidti*, *D. perspicillatus*, *D. trachops*, *Melamphaes danae*, and *Bregmaceros japonicus* and dashed lines for *Triphoturus nigrescens* and *D. fragilis* are drawn from equations determined by least squares regression on measurements from five or more specimens of each species over the size ranges plotted; coefficients of determination (r^2) exceeded 0.80 for all except *Diogenichthys atlanticus* ($r^2 = 0.62$). *Notolychnus valdiviae* ($r^2 = 0.23$) is represented by the area enclosed by points from five specimens.

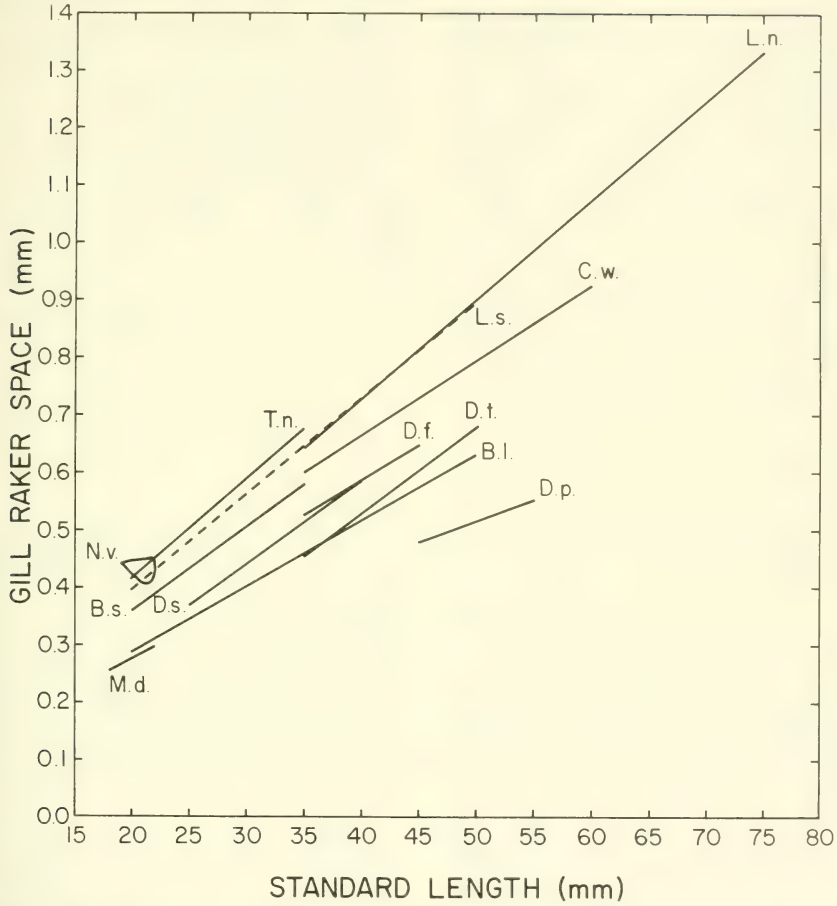


FIGURE 3.—Relationships between standard length and average space between gill rakers on the lower branch of the first gill arch for 12 species of mesopelagic fishes designated by initials of genus and species names. Lines for *Lampanyctus nobilis*, *Triphoturus nigrescens*, *Ceratoscopelus warmingi*, *Benthosema suborbitale*, *Bolinichthys longipes*, *Diaphus schmidti*, *D. perspicillatus*, *D. fragilis*, *D. trachops*, and *Melamphaes danae* and dashed line for *Lampanyctus steinbecki* are drawn from equations determined by least squares regression on measurements from five or more specimens of each species over the size ranges plotted; coefficients of determination (r^2) exceeded 0.80 for all except *M. danae* ($r^2 = 0.78$). The equation for *Diogenichthys atlanticus* ($r^2 = 0.60$) was almost identical with that for *M. danae* and was omitted for clarity. *Notolychnus valdiviae* ($r^2 = 0.04$) is represented by the area enclosed by points from five specimens.

most similar species were *Lampanyctus steinbecki*, *L. nobilis*, *T. nigrescens*, and *Notolychnus valdiviae*. All ate relatively large and opaque or pigmented prey. Both within and between species, the sizes of the most frequent and most preferred prey were roughly correlated with standard length, i.e., the large *L. nobilis* favored euphausiids and large copepods, while *N. valdiviae* and the small *L. steinbecki* and *T. nigrescens* preferred some types as small as *Oncaea*. All four species had relatively small eyes and relatively large gill raker gaps, and three had relatively low gill raker "areas." The gill

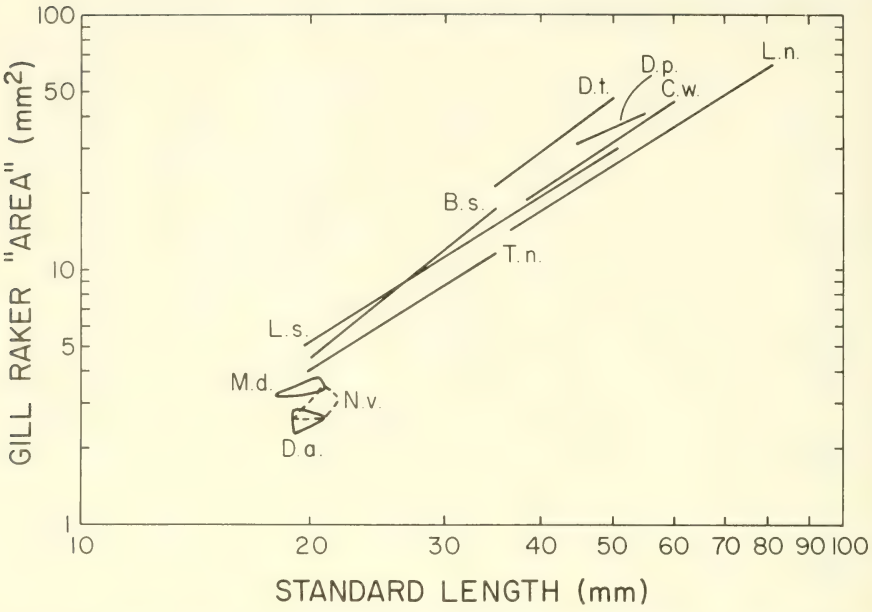


FIGURE 4.—Relationships (on logarithmic scales) between standard length and gill raker "area" (see text) for 10 species of mesopelagic fishes designated by initials of genus and species names. Lines for *Lampanyctus steinbecki*, *L. nobilis*, *Triphoturus nigrescens*, *Ceratoscopelus warmingi*, *Benthosema suborbitale*, *Diaphus perspicillatus*, and *D. trachops* are drawn from equations determined by least squares linear regression on the logarithms of the data from five or more specimens of each species over the size ranges plotted; coefficients of determination (r^2) exceeded 0.89 for all shown and also for *Bolinichthys longipes*, *D. schmidti*, and *D. fragilis* whose relationships were so similar to those of one or more species illustrated that they were omitted for clarity. *Notolychnus valdiviae* (r^2 = 0.26, dashed lines) and *Diogenichthys atlanticus* (r^2 = 0.09) and *Melamphaes danae* (r^2 = 0.23) are represented by the areas enclosed by points from five specimens each.

rakers of all four were thin, cylindrical in cross section, and covered with short rasplike teeth; while those of the other species were flattened usually with sawlike teeth on the leading edge. Thus these species seem best adapted for detecting the more visible prey and for retaining only relatively large items.

Ceratoscopelus warmingi and *D. perspicillatus* had the largest lenses of any species and sizes considered. For both species the ASV's of many types of prey were high, indicating that they are capable of searching greater volumes than species with smaller lenses. *Ceratoscopelus warmingi*, however, preferred relatively large prey while *D. perspicillatus* showed high ASV's for small as well as large types. Consonant with these differences in diet, *C. warmingi* had a relatively larger gape and less closely spaced gill rakers than did *D. perspicillatus*.

Diogenichthys atlanticus, *Benthosema suborbitale*, *Bolinichthys longipes*, and *Diaphus trachops* also had relatively large lenses; if *Diogenichthys atlanticus* or *Benthosema suborbitale* grew as large as *C. warmingi* or *Diaphus perspicillatus*, their lenses would be larger. The first three species' diets included high fractions of microzooplankton. *Diogenichthys atlanticus*, which had the largest relative lens size and smallest gape, had eaten the widest variety of microzooplankton including many forms probably less visible than the *Oncaea* spp., which dominated the microzooplankton eaten by *B. suborbitale* and *Bolinichthys longipes*. *Bolinichthys longipes*, which was the only species which ate the small

Oncaea spp. (≤0.6 mm) frequently and had the lowest fractions of macrozooplankton, had much finer gill rakers and somewhat larger lenses than similar-sized *Benthosema suborbitale*, which took a wider variety of sizes. *Diaphus trachops*, in contrast to the other three, ate mostly large prey. ASV's of most of its prey were also much higher than those of the other species. Its gape was the largest of all species examined, consonant with large prey size, but its relatively finely spaced gill rakers and high raker area indicate it is equipped to retain small prey as well. *Diaphus trachops* was the only species caught only at 170 m where zooplankton densities and particularly microzooplankton were much lower. While the large lenses of the other three species seem related to increased ability to detect small prey, *D. trachops*' seem related to detection of relatively large, less dense prey from greater distances. Lower light levels in its depth range would also favor large lenses.

Diaphus schmidti and *D. fragilis* were similar to each other other and intermediate to other myctophids in all four features. Diet of *D. schmidti* was generally similar to that of *D. perspicillatus*, i.e., very general, but it differed in that high ASV's were not associated with many types of small copepods preferred by *D. perspicillatus*. This is consonant with *D. perspicillatus*' much finer gill rakers and larger lenses. Although data are few, the diet of *D. fragilis* seems most similar to that of *D. schmidti*. *Diaphus fragilis* is uncommon near Hawaii but very abundant in more productive waters near the Equator (Hartmann and Clarke 1975). It is also larger than *D. schmidti*. Ebeling (1962) has suggested that "dwarf" species of melamphaids are adapted to the less productive central water masses. The above indicates that similarly the larger of two otherwise similar myctophids is less successful in the central water mass.

Bregmaceros japonicus was the most distinct morphologically of all species considered. It had no gill rakers and the smallest lenses and gape of all species. Though it ate chaetognaths fairly frequently, the ASV's indicated that it prefers large crustaceans. Apparently the small mouth of this species does not inhibit it from ingesting large prey, and in spite of its small lenses, it is able to detect and capture at least a fraction of the translucent chaetognaths encountered.

Diet of *M. danae* was quite distinct from that of the others. The most frequent and preferred items included large and small forms and taxa other than crustaceans—many of which were rarely eaten by other fishes. Also, certain prey such as *Pleuromamma* and *Oncaea* spp., which appeared in diets of almost all other fishes, were absent or nearly so from that of *M. danae*. Not a great deal can be gleaned from its morphological features; in spite of its small mouth and lens, *M. danae* is obviously capable of ingesting fairly large items and detecting small or translucent prey, but there is no clear indication of why certain prey types were not eaten.

Among the myctophids, differences in lens size and gill raker space were most obviously and frequently correlated with differences in diet and preference. These indicate that ability to visually detect and to retain prey in the mouth are important factors affecting frequency and preference. The general lack of correlation of dietary features with differences in gill raker area indicates these fish are probably not simply filtering. Morphological relationships within the myctophids, however, do not seem to extend to the sole representatives of the other two families considered here. *Bregmaceros japonicus* and *M. danae* appear basically different; whether their morphological features are in any way related to diet must await data on other species of these families.

Aside from the correlations of lens size with diet and lack thereof for gill raker area, the preferences observed and absolute values of ASV's also indicate that these fishes feed in a particulate, visually oriented mode (O'Connell 1972) as opposed to filtering. That the fishes are selective precludes simple filtration unless it is assumed that the differences between diet and available prey are due entirely to differential escape capabilities of the prey, and the general absence of small or translucent prey from the diets implicates vision. In many cases, the ASV's, which are minimal estimates of the volume searched, seem too high to have resulted from filtering alone. Even assuming that the area filtered is as large as the square of the premaxillary and that the fish swam at 2.5 body lengths/s (Ware 1978) for 5 h, a 50 mm *D. trachops*, *C. warmingi*, *D. perspicillatus*, or *L. steinbecki* would search only 0.25-0.32 m^3 (depending on premaxillary length). Yet ASV's were as high as 1.0 m^3 for several prey of these species. To search 1.0 m^3 visually would require that the fish detect prey within only about 12 mm. Similarly, a 20 mm *Diogenichthys atlanticus* could at best filter only about 0.008 m^3, while ASV's of at least five times this were associated with several of

its prey. Even the smaller and therefore slower *D. atlanticus* would have to detect prey only within about 19 mm to search 1.0 m^3 in the same time.

Comparison of my results with those of other studies is limited to generalizations due to different methodologies. In most other studies, prey items have been identified only to major taxa, bias due to differential digestion has not been considered, and diets have not been compared with appropriate estimates of available prey densities.

Legand and Rivaton (1969) gave diets of nine comparable species from the tropical Indian Ocean. As near Hawaii, crustaceans dominated the diets, and except for higher proportions of amphipods and lower proportions of ostracods, the diets of the myctophids were similar to those of congeners from Hawaii. *Ceratoscopelus "townsendi"* (which is probably really *C. warmingi*) had a wide variety of prey and with the two *Lampanyctus* spp. had the highest frequency of euphausiids. The diet of *Benthosema simile*, the only species for which copepod genera were given, was quite similar to that of *B. suborbitale*. *Bregmaceros macclellandi*, unlike *B. japonicus* from Hawaii, had eaten no chaetognaths. Merrett and Roe's (1974) data on three myctophid species from the subtropical Atlantic also indicate that crustaceans were the most important prey. Diets of the individual species appear generally similar to those of the most closely related species considered from Hawaii.

Gorelova (1978) found that migratory crustaceans dominated the diets of both *C. warmingi* and *Bolinichthys longipes* in the western equatorial Pacific. The diet of small *C. warmingi* was dominated by copepods, and most items were <4 mm long, but specimens of sizes comparable to those examined in my study (40-90 mm total length) had eaten a wider variety of prey, over 50% of which (by weight) were >4 mm. The dominant euphausiids were the large *Thysanopoda* and *Nematobrachion* spp. The diet of all sizes of *B. longipes* was dominated by copepods, and the euphausiids eaten were mostly the smaller *Euphausia* and *Stylocheiron* spp. *Oncaea* spp. were much less important than near Hawaii. Among the large copepods, however, candaciids were the dominant type in both areas. Gorelova (1977) noted that *Lampanyctus* and *Triphoturus* (species not given) in the equatorial Pacific eat euphausiids almost exclusively.

Baird et al. (1975) showed that *Diaphus taaningi* in the Cariaco Trench, like two Hawaiian *Diaphus* spp., ate a wide variety of prey, but in contrast to all other species considered here or elsewhere, the diet was heavily dominated by *Oikopleura*. Since *Oikopleura* is probably rendered unrecognizable in the stomach faster than most of the other prey types, its importance in the diet is probably even greater than Baird et al.'s data indicate. Its frequency in the plankton from the cod end of the trawl was much lower than in the diet; however, it was probably underrepresented relative to larger forms in such a sample. Whether the dominance of *Oikopleura* reflects a real preference or simply very high densities at the depths where the fish were feeding cannot be determined.

Tyler and Percy (1975) investigated three species of myctophids from off Oregon. The diets of all three were heavily dominated by euphausiids, mostly *E. pacifica* which was the most abundant species in the area, and medium to large copepods, the most frequently identified of which were *Calanus* and *Metridia* spp. There was little indication of differences between fish species. Gjösaeter (1973) showed similar results for another high latitude myctophid, *Benthosema glaciale*; in this case *Thysanoessa* spp. were the dominant euphausiids.

The results of most studies generally agree that, with the obvious exception of *D. taaningi*, vertically migrating fishes feed primarily upon relatively large, probably more visible crustacean zooplankton; however, the data for some species considered here and by Gorelova (1978) indicate that small juveniles graze the microzooplankton more heavily than sizes considered by most studies. In contrast to the neustonic myctophids, e.g., *Centrobranchus* and certain *Myctophum* spp., which feed primarily on shallow-living zooplankton (Gorelova 1977), the principal prey of the species considered here and by most other studies undertake substantial diel vertical migrations themselves (Brinton 1967; Roe 1972)—some almost as extensive as those of the fishes—and are not present in the epipelagic by day.

Though the diets of the 14 species considered here show some general similarities, differences in frequency of and preference for different prey types indicate that most species are at least somewhat specialized. The discussion of diet and morphology above points out unique features for most species. *Lampanyctus steinbecki*, *L. nobilis*, *Triphoturus nigrescens*, and *Notolychnus valdiviae* were the only species which were very simi-

lar to each other, but quite distinct from the others. Differences in size and depth distribution at night probably reduce diet overlap among these species. *Triphoturus nigrescens* and *L. nobilis* occur shallower than do *N. valdiviae* and *L. steinbecki*, and within each pair, one species is considerably larger than the other. Other multispecies studies in the tropical or subtropical open ocean also indicate some degree of specialization among cooccurring species.

In contrast, Tyler and Pearcy's (1975) results indicate that high latitude species have little or no separation or specialization in diet. Confirmation and further documentation of the apparent difference are certainly merited. If true, it could indicate that tropical species are less likely to be competing against each other for food or that species in the highly productive waters off Oregon are not food limited. The apparent difference in degree of dietary specialization also has obvious implications relevant to differences in diversity—both of the fish faunas and of their prey—between tropical and temperate oceanic communities.

ACKNOWLEDGMENTS

This research was supported by NSF GA-38423 and the Hawaii Institute of Marine Biology, University of Hawaii. I thank the officers and crew of the research vessels *Teritu* and *Moana Wave*; the staff of Ship Operations, Hawaii Institute of Geophysics; and the many people who participated on the cruises for their assistance and cooperation. Patricia J. Wagner capably assisted in the early phases of the work. Euphausiids and decapods were identified by K. Gopalakrishnan.

LITERATURE CITED

AHLSTROM, E. H.
1969. Mesopelagic and bathypelagic fishes in the California Current region. Calif. Coop. Oceanic Fish. Invest. Rep. 13:39-44.

BAIRD, R. C., T. L. HOPKINS, AND D. F. WILSON.
1975. Diet and feeding chronology of *Diaphus taaningi* (Myctophidae) in the Cariaco Trench. Copeia 1975: 356-365.

BRINTON, E.
1967. Vertical migration and avoidance capability of euphausiids in the California Current. Limnol. Oceanogr. 12:451-483.

CHESSON, J.
1978. Measuring preference in selective predation. Ecology 59:211-215.

CLARKE, T. A.
1973. Some aspects of the ecology of lanternfishes (Myctophidae) in the Pacific Ocean near Hawaii. Fish. Bull., U.S. 71:401-434.
1974. Some aspects of the ecology of stomiatoid fishes in the Pacific Ocean near Hawaii. Fish. Bull., U.S. 72:337-351.
1978. Diel feeding patterns of 16 species of mesopelagic fishes from Hawaiian waters. Fish. Bull., U.S. 76:495-513.

CLARKE, T. A., AND P. J. WAGNER.
1976. Vertical distribution and other aspects of the ecology of certain mesopelagic fishes taken near Hawaii. Fish. Bull., U.S. 74:635-645.

EBELING, A. W.
1962. Melamphaidae. I. Systematics and zoogeography of the species in the bathypelagic fish genus *Melamphaes* Günther. Dana Rep. Carlsberg Found. 58, 164 p.

FROST, B. W., AND L. E. MCCRONE.
1979. Vertical distribution, diel vertical migration, and abundance of some mesopelagic fishes in the eastern subarctic Pacific Ocean in summer. Fish. Bull., U.S. 76:751-770.

GANNON, J. E.
1976. The effects of differential digestion rates of zooplankton by alewife, *Alosa pseudoharengus*, on determinations of selective feeding. Trans. Am. Fish. Soc. 105:89-95.

GJOSAETER, J.
1973. The food of the myctophid fish, *Benthosema glaciale* (Reinhardt), from western Norway. Sarsia 52:53-58.

GORELOVA, T. A.
1975. The feeding of fishes of the family Myctophidae. J. Ichthyol. 15:208-219.
1977. Some characteristics of the nutrition of the young of nictoepipelagic and mesopelagic lantern fish (Pisces, Myctophidae). Oceanology 17:220-222.
1978. Nutrition of the luminescent anchovies *Ceratoscopelus warmingi* (Lütken) and *Bolinichthys longipes* (Brauer) Fam. Myctophidae in the western equatorial part of the Pacific Ocean. J. Ichthyol. 18:673-683.

HARTMANN, A. R., AND T. A. CLARKE.
1975. The distribution of myctophid fishes across the Central Equatorial Pacific. Fish. Bull., U.S. 73:633-641.

HOPKINS, T. L., AND R. C. BAIRD.
1975. Net feeding in mesopelagic fishes. Fish. Bull., U.S. 73:908-914.

IVLEV, V. S.
1961. Experimental ecology of the feeding of fishes. Yale Univ. Press, New Haven, Conn., 302 p.

LEGAND, M., AND J. RIVATON.
1969. Cycles biologiques des poissons mésopélagiques de l'est de l'Océan Indien. Troisième note: Action prédatrice des poissons micronectoniques. Cah. O.R.S.T.O.M., sér. Océanogr. 7(3):29-45.

MAYNARD, S. D., F. V. RIGGS, AND J. F. WALTERS.
1975. Mesopelagic micronekton in Hawaiian waters: Faunal composition, standing stock, and diel vertical migration. Fish. Bull., U.S. 73: 726-736.

MERRETT, N. R., AND H. S. J. ROE.
1974. Patterns and selectivity in the feeding of certain mesopelagic fishes. Mar. Biol. (Berl.) 28:115-126.

O'BRIEN, W. J., N. A. SLADE, AND G. L. VINYARD.
1976. Apparent size as the determinant of prey selection by bluegill sunfish (*Lepomis macrochirus*). Ecology 57:1304-1310.

O' CONNELL, C. P.
1972. The interrelation of biting and filtering in the feeding activity of the northern anchovy (*Engraulis mordax*). J. Fish. Res. Board Can. 29:285-293.

PEARCY, W. G., AND R. M. LAURS.
1966. Vertical migration and distribution of mesopelagic fishes off Oregon. Deep-Sea Res. Oceanogr. Abstr. 13:153-165.

ROE, H. S. J.
1972. The vertical distributions and diurnal migrations of calanoid copepods collected on the SOND Cruise, 1965. I. The total population and general discussion. J. Mar. Biol. Assoc. U.K. 52:277-314.

TYLER, H. R., JR., AND W. G. PEARCY.
1975. The feeding habits of three species of lanternfishes (family Myctophidae) off Oregon, USA. Mar. Biol. (Berl.) 32:7-11.

WARE, D. M.
1978. Bioenergetics of pelagic fish: Theoretical change in swimming speed and ration with body size. J. Fish. Res. Board Can. 35:220-228.

ZAHURANEC, B. J., AND W. L. PUGH.
1971. Biological results from scattering layer investigations in the Norwegian Sea. *In* G. B. Farquhar (editor), Proceedings of an international symposium on biological sound scattering in the ocean, p. 360-380. U.S. Gov. Print. Off., Wash., D.C.

ZARET, T. M., AND W. C. KERFOOT.
1975. Fish predation on *Bosmina longirostris*: Body-size selection *versus* visibility selection. Ecology 56:232-237.

SURVIVAL, SIZE, AND EMERGENCE OF PINK SALMON, *ONCORHYNCHUS GORBUSCHA*, ALEVINS AFTER SHORT- AND LONG-TERM EXPOSURES TO AMMONIA

STANLEY D. RICE AND JACK E. BAILEY[1]

ABSTRACT

Eggs and alevins of pink salmon, *Oncorhynchus gorbuscha*, were exposed to ammonia in a series of static and flow-through experiments to determine what levels of ammonia would decrease survival. Short-term acute toxicity tests (96 hours) were conducted at several stages in development to determine which of the early life stages were most sensitive to ammonia. Long-term tests (up to 61 days) with lower ammonia concentrations were conducted to determine effects on survival and size of fry at emergence. The possibility of ammonia stimulating emergence of immature fry was tested at various stages of development.

Pink salmon alevins were most sensitive at the completion of yolk absorption, when the 96-hour median tolerance limit was 83 parts per billion of un-ionized ammonia. Concentrations as low as 1.2 parts per billion reduced fry length in the 61-day exposures. Only levels above 10 parts per billion of ammonia stimulated early emergence of immature fry.

The concentrations of ammonia causing any of the deleterious effects observed are greater than concentrations observed in the hatchery or the natural environment.

Ammonia is a natural waste product of protein catabolism and can be toxic to aquatic organisms under certain conditions. Ammonia exists in the water in two forms, un-ionized NH_3 and ionized NH_4^+; the NH_3 is much more toxic than NH_4^+ (European Inland Fisheries Advisory Commission 1970). The percentage of ammonia in the more toxic form, NH_3, is influenced primarily by pH of the water and by factors that influence pH, e.g., temperature, carbon dioxide, and bicarbonate alkalinity (European Inland Fisheries Advisory Commission 1970).

Much information is available on the toxicity of ammonia to fishes, including juvenile and adult salmonids; but it is surprising that little information exists on the toxicity of ammonia to fertilized eggs and larvae of teleosts, especially because these life stages are often assumed to be relatively sensitive. In acute toxicity studies, trout eggs and alevins[2] are much more tolerant to ammonia than fry (Penaz 1965; Rice and Stokes 1975). Long-term studies of larval and juvenile forms exposed to ammonia are virtually nonexistent; but in one long-term study Burkhalter and Kaya (1977) continuously exposed rainbow trout, *Salmo gairdneri*, eggs and alevins to ammonia until the end of yolk absorption (about 67 d). They found retardation of growth at the lowest concentrations tested and other adverse effects at higher concentrations.

Toxicity of NH_3 to the early life stages of salmon in the northern latitudes would not be a problem because low temperature and pH cause most of the ammonia (99+%) in the water to be in the less toxic form, NH_4^+. However, salmon eggs and alevins in subarctic latitudes have a long developmental life history in an intragravel stream environment (up to 8 mo) where intragravel waterflow can be reduced for several months during the winter because of low temperatures. The low waterflow may not be sufficient to prevent a buildup of excreted ammonia in the water layer immediately adjacent to the developing egg or alevin. Ammonia levels may rise during these periods of low flow to concentrations that are deleterious to survival, health, and/or growth of the developing salmon.

Our study had three specific objectives: 1) to determine the sensitivities (judged by survival) of early life stages of pink salmon, *Oncorhynchus*

[1]Northwest and Alaska Fisheries Center Auke Bay Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 155, Auke Bay, AK 99821.

[2]After hatching, alevins (salmon larvae) reside in the spawning gravels for several months while consuming their large yolks. Salmon alevins that have no externally visible yolk ("buttoned up") become fry when they inflate their swim bladder and become free-swimming; this occurs immediately after volitional emergence from natural redds and gravel incubators.

Manuscript accepted January 1980.
FISHERY BULLETIN: VOL. 78, NO. 3, 1980.

gorbuscha, to short-term, high concentrations of NH_3; 2) to determine the size of emergent fry after long-term exposure of alevins to low concentrations of NH_3; and 3) to determine whether early emergence of immature salmon fry can be caused by short-term sublethal concentrations of NH_3. The short-term tests with high concentrations of NH_3 identified the more sensitive life stages and provided information on concentrations that were lethal. The sublethal tests identified NH_3 concentrations that caused decreases in the size of emergent fry or caused early emergence of immature fry. Identification of factors that cause smaller fry at emergence is important because smaller fry are less capable of surviving in the environment. Laboratory and field studies by Bams (1967) and Parker (1971) have shown that smaller salmon fry have less swimming endurance and are selectively preyed upon by larger predators.

Our ultimate objective was to compare the concentrations of NH_3 that are harmful to pink salmon in the laboratory with concentrations of NH_3 that are harmful in hatchery incubators (Bailey et al. 1980) and in natural spawning redds (Rice and Bailey 1980). To compare the studies of Bailey et al. and Rice and Bailey with our study, our tests were conducted with pink salmon eggs, alevins, and fry exposed to NH_3 at temperatures $<4.8°$ C and pH's <6.5—conditions that are typical for freshwater streams in boggy rain forests of the colder northern latitudes.

MATERIALS AND METHODS

The pink salmon eggs were fertilized in September at Lovers Cove Creek, southern Baranof Island, southeastern Alaska, and incubated to the eyed stage in Heath[3] incubators at Auke Bay, near Juneau, Alaska. Some eyed eggs were taken from the Heath incubators and placed in upwelling incubator cups or in 15.2 cm diameter pipe incubators (Rice and Moles[4]) for long-term exposures or emergence stimulation tests. The rest of the eggs were left in the Heath incubators for short-term bioassays.

We measured concentrations of total ammonia ($NH_3 + NH_4^+$) by an automated method that measured the intensity of indophenol blue formed after the reaction of ammonia with alkaline phenol hypochlorite (U.S. Environmental Protection Agency 1974). Total ammonia concentrations were analyzed the same day water samples were taken. The concentrations reported in this study are for the toxic, un-ionized NH_3. Total ammonia was measured and the concentration of NH_3 determined by using the temperature-pH correction tables of Emerson et al. (1975).

Our experimental approach involved three types of experiments: 1) to determine the sensitivity (survival) of each early life stage to NH_3, we exposed eyed eggs, alevins, and fry to short-term, high concentrations of NH_3 (>50 ppb); 2) to determine the effect of long-term exposures of NH_3 on size of fry at emergence (end of yolk absorption), we exposed alevins at different stages of development to low concentrations of NH_3 (<3 ppb) for up to 61 d; and 3) to determine whether NH_3 would cause emergence of immature fry, we exposed alevins to high concentrations of NH_3 (30-150 ppb) for 24 h and counted voluntary out-migrants from the incubators.

The senstivities of different life stages to short-term, high concentrations of NH_3 were tested with 96-h bioassays conducted according to the standard procedures of Doudoroff et al. (1951). Eggs, alevins, and fry were exposed to static solutions of ammonium sulfate in freshwater at pH of 6.3-6.5 and 3.7°-4.8° C. Twenty-five animals were placed in each 18 l test container; resulting ratios of tissue to test solution were <0.3 g/l. The test solutions were aerated and the tests were conducted in the dark. Median tolerance limits (TLm's) and associated 95% confidence levels were calculated by a computerized probit analysis program based on the method discussed by Finney (1971).

To test the effect of long-term exposures to NH_3 on size of fry at emergence, ammonium sulfate was introduced into the water which flowed through incubator cups containing the developing alevins. Twenty-five eyed eggs were placed in each upwelling incubator cup (Bailey[5]), and exposures to NH_3 began at selected times after hatching. The NH_3 was introduced by dripping small quantities of concentrated ammonium sulfate solutions into

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[4]Rice, S. D., and D. A. Moles. 1977. Apparatus for incubating salmonid eggs and alevins in a variety of controlled environments for laboratory studies. Unpubl. manuscr. Northwest and Alaska Fisheries Center Auke Bay Laboratory, NMFS, NOAA, Auke Bay, AK 99821.

[5]Bailey, J. E. 1964. Incubation of pink salmon eggs in a simulated intertidal environment. *In* Proceedings 15th Annual Northwest Fish Culture Conference, p. 79-89. Oregon Agricultural Experiment Station, Corvallis, OR 97330.

the incoming water line to each cup. Flow rates of both water and ammonium sulfate were kept constant by using supplies with a constant head. We measured flow rates daily and concentrations of total ammonia in each cup twice each week.

In the long-term tests, three groups of alevins (A, B, and C) were exposed to ammonium sulfate solutions for three different lengths of time. Group A was exposed for the 21 d preceding the completion of yolk absorption (time of normal emergence and migration). Group B was exposed for 40 d, with the exposure ending 21 d before yolk absorption. Group C was exposed for 61 d before yolk absorption. In each group, subgroups of alevins were exposed to concentrations of NH_3 ranging from 0 (control) to 4 ppb.

At the end of the long-term exposures when control fry had absorbed all visible yolk, 50 fry from each NH_3 exposure were sampled and preserved in 5% Formalin. Size was determined after 6 wk when tissue hydration adjustments were stable. After blotting the fry with a damp paper towel, fork lengths were measured to the nearest millimeter and weights to the nearest milligram. Mean K_D developmental indices (Bams 1970) were 1.99 for the controls and 1.96-2.07 for the groups exposed to NH_3; therefore, fry were at similar developmental stages and the size of fry from the various groups could be compared directly with the size of controls. Data are reported as means ±95% confidence intervals.

In another experiment, the possible stimulation of early emergence of immature fry was tested by exposing alevins in gravel incubators to a single exposure of NH_3 for 24 h at various times during development. Concentrated ammonium sulfate solutions were pumped into the intake lines of small experimental gravel incubators (Rice and Moles footnote 4) at rates sufficient to produce desired concentrations of NH_3. Alevins or fry were trapped if they voluntarily emerged during the exposure. The numbers of fry and stage of development were noted daily. Pink salmon were judged to have emerged early when they emerged before control fry and were judged to have emerged prematurely if yolk sacs were visible externally. Pipe incubators with a volume of 5 l and a water flow of 450 ml/min were seeded in November with 300 eyed eggs each. Each week after hatching, several incubators were exposed to four different concentrations of NH_3 for 24 h. Each incubator received only one 24-h treatment and different sets of incubators were used for the NH_3 exposures that were performed every week during the 2 mo prior to emergence of controls. All NH_3 concentrations were measured analytically by the method previously described.

SENSITIVITY OF DIFFERENT LIFE STAGES TO AMMONIA

Late alevins near emergence were the most sensitive of all life stages tested to short-term, acute concentrations of NH_3 (Figure 1). Eyed eggs exposed for 96 h to toxicants in December were not harmed by concentrations >1,500 ppb and appeared to hatch normally. Late alevins (tested 13-17 March) had the lowest 96-h TLm measured, 83 ppb of NH_3. The fry (tested on 10-14 April) had been feeding for 2 wk and appeared to have slightly greater tolerance to NH_3 than the alevins tested just prior to emergence, but the differences between the tests were not statistically significant. Greater sensitivity just prior to emergence is consistent with similar observations of trout eggs and alevins exposed to ammonia (Penaz 1965; Rice and Stokes 1975). Studies with other toxicants have identified eggs to be much more tolerant than alevins (Wurtz-Arlet 1959; Garrison 1968; Rice et al. 1975).

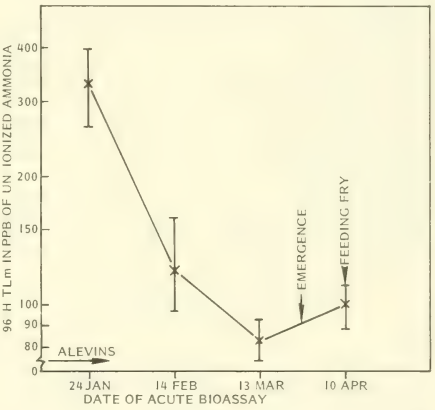


FIGURE 1.—96-h median tolerance limits (TLm's) and ±95% confidence limits of pink salmon alevins and fry exposed during short-term, acute experiments to un-ionized ammonia (NH_3). Eggs were also tested, but no mortalities were observed at the highest concentration (1,500 ppb NH_3).

EFFECT OF LONG-TERM AMMONIA EXPOSURES ON SIZE OF FRY AT EMERGENCE

Lengthy exposure of alevins to NH_3 resulted in fry that were smaller than control fry at emergence (Figure 2). Although the three test groups of alevins (groups A, B, and C) were exposed to NH_3 for different time periods (21, 40, and 61 d), they were all sampled when the control groups had completed yolk absorption. The highest exposure concentration of NH_3 (4 ppb) caused significant decreases in weight ($P<0.05$) of exposed fry in all three exposure groups. At exposure concentrations <4 ppb, the groups held for 40 d and 61 d (B and C) were similar in response: both were significantly smaller in length and weight after exposure to 2.4 ppb NH_3; after exposure to 1.2 ppb there was no significant difference. Effects were consistently more adverse for group C, the group receiving the longest exposures. The statistically significant decrease in weight ($P<0.05$) of one observation of group A exposed to 0.2 ppb of NH_3 appeared to be an aberrant observation.

EFFECT OF AMMONIA ON EARLY EMERGENCE

Short-term (24 h) exposures to low concentrations of NH_3 (<25 ppb) did not stimulate early emergence during or immediately after the exposures; emergence patterns were the same as those of unexposed fry. At higher concentrations (30-50 ppb) of NH_3, early emergence of the alevins (up to 11%) occurred within 24 h of exposures, but little residual effect was observed later when 50% emerged at approximately the same date as unexposed alevins (Figure 3). Some early emergence of the alevins (up to 12%) occurred at high concentrations of 100-150 ppb NH_3, but massive early emergence was not observed even though these concentrations were above the 96-h TLm's for alevins or fry during the period 15 February to 10 April (Figure 1). Although the high concentrations were probably stressful, mortalities never exceeded 4%. In all cases, when early emergence was stimulated, it occurred within 24 h of the beginning of exposure. In response to the acute exposures to NH_3, the alevins that emerged early had visible amounts of yolk, indicating they were not ready for normal emergence. The alevins that did not emerge during or immediately after NH_3 exposures stayed in the incubators almost as long as the unexposed alevins and emerged without any visible yolk.

IMPLICATIONS OF AMMONIA EXPOSURE STUDIES

Ammonia exposures resulting in immature or small fry would be detrimental to the survival of pink salmon fry because these small fish are easily preyed upon (Bams 1967; Parker 1971). We did observe some early emergence of immature fry during or immediately after short-term exposures to NH_3, but only at the high concentrations that aproached highly toxic levels. These high concentrations are not likely to be encountered in natural or hatchery environments, but if they were encountered, the immature alevins that emerged with visible yolk would have difficulty swimming and avoiding predators.

We do not know the effect of long-term exposures to low concentration of NH_3 on time of voluntary emergence, but these tests do produce emergent fry with decreased weight and length. Exposed emergent fry have increased metabolic rate and, therefore, increased demand on yolk reserves and less yolk reserve available for incorporation into developing tissues. Adult trout exposed to NH_3 have increased metabolic rates, and NH_3 probably has the same toxic action in fishes that it has in mammals—impairment of cerebral energy metabolism (Smart 1978).

The lowest concentration of NH_3 that caused fry to be significantly smaller in length and weight at emergence was 2.4 ppb (61- and 40-d exposures) (Figure 2). This concentration is about one-twentieth of the concentration (50 ppb) that caused retardation of growth in rainbow trout fry that had been exposed continuously for about 67 d from the beginning of the egg stage (Burkhalter and Kaya 1977). Pink salmon alevins exposed to NH_3 for 61 d at 4° C in our study were more sensitive (as judged by effects on size) than the faster developing rainbow trout eggs and alevins exposed for about 67 d at 12° C. In the trout study (Burkhalter and Kaya 1977), 25 d of the 67-d exposure were during the egg stage, a stage that is relatively tolerant compared with the alevin stage.

The highest concentrations of NH_3 in the discharge water of a hatchery incubator with an abnormally high density of pink salmon alevins (Bailey et al. 1980) was 0.14 ppb, and the highest concentration from intragravel water of a stream

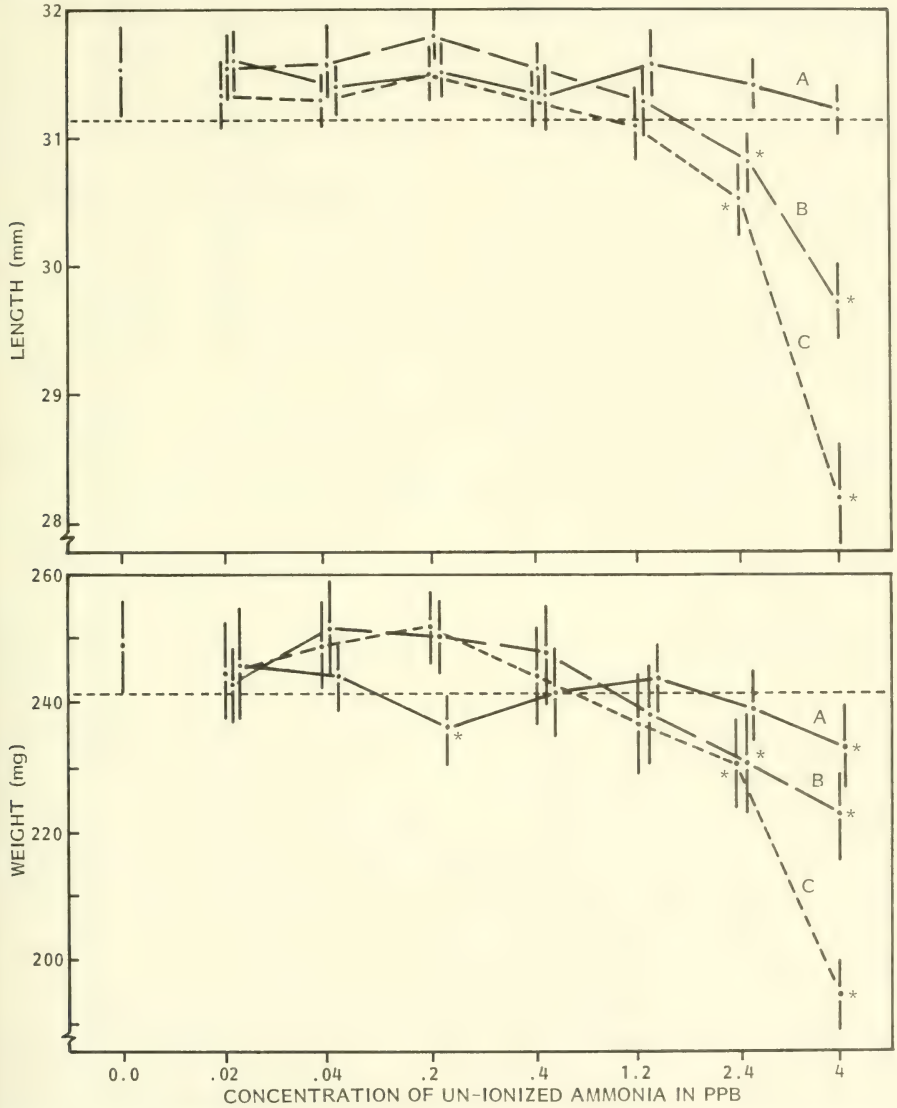


FIGURE 2.—Length (upper) and weight (lower) of migrant pink salmon fry at emergence resulting from groups of alevins exposed to various concentrations of un-ionized ammonia (NH_3) for three lengths of long-term exposure. For each mean, $n = 50$ fry, bars indicate 95% confidence limits. Group A—exposed for 21 d just prior to migration; group B—exposed for 40 d, ending 21 d prior to migration; group C—exposed for 61 d continuously until migration. Asterisks indicate significant differences in length or weight ($P < 0.05$) between those fry that had been exposed and control fry.

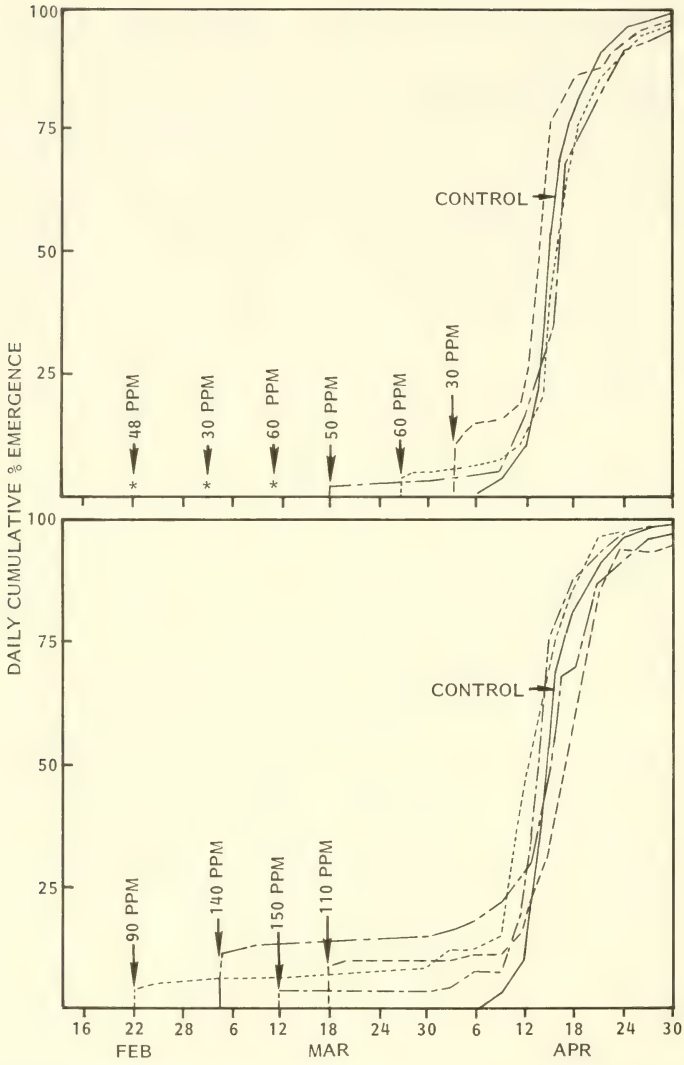


FIGURE 3.—Daily cumulative percent of emergence of pink salmon fry that did not receive exposure to ammonia (controls) or received a single 24-h exposure to ammonia sometime prior to normal emergence. The dates when the 24-h exposures began are indicated by arrows and exposure concentrations. Three ranges of un-ionized ammonia concentrations were used: 1) <25 ppb (not shown) which resulted in <1% immediate emergence. The date of 50% emergence was within ±3 d of 50% control emergence, 2) 30-60 ppb of un-ionized ammonia (upper), 3) 90-150 ppb of un-ionized ammonia (lower). Asterisk indicates the lack of initial emergence (<1%) in response to ammonia exposures (same pattern as controls).

with known densities of pink salmon alevins (Rice and Bailey 1980) was 0.096 ppb. Both of these "real life" extremes of NH_3 were much less than the concentrations we found to cause early emergence of immature fry and acute toxicity. The concentrations that caused small size after lengthy exposure in this study were about 10 times greater than the maximum concentrations found in hatchery incubator effluents and intragravel water from salmon redds (Bailey et al. 1980; Rice and Bailey 1980). Thus, exposure to naturally occurring ammonia is not a likely problem for salmon eggs and alevins in Alaska under natural or hatchery conditions where temperatures are low and waters are acidic—conditions that cause the percentage of NH_3 to be very low ($<0.1\%$).

If pink salmon are reared at higher temperatures and alkalinities, the potential for adverse effects from NH_3 is increased because of the shift in the equilibrium toward NH_3. At 5° C and pH of 7.5, 0.394% of the total ammonia is NH_3; in contrast, at 5° C and pH of 6.5, 0.0395% is NH_3 (Emerson et al. 1975). Therefore, if the pH of Auke Creek and Sashin Creek were 7.5 rather than 6.5, approximately 10 times more NH_3 might have been observed. The level of total ammonia would have been the same, but the percentage of NH_3 would have been much greater. Assuming no losses from aeration or other factors, the percentage of NH_3 would be about 100 times greater at a pH of 8.5 than at a pH of 6.5. It is possible that high densities of alevins in hatcheries or stream gravels could produce unhealthy concentrations of NH_3 if the pH is alkaline. From our exeriments, we conclude that concentrations of NH_3 >0.50 ppb should be avoided. Because our results were generated at relatively low temperature and pH, extrapolation of our data to extreme situations of temperature >10° C or pH >7.8 is inappropriate.

ACKNOWLEDGMENTS

Sidney G. Taylor aided in the 61-d tests and the length-weight analysis. Charlotte Misch conducted the tests on early emergence.

LITERATURE CITED

BAILEY, J. E., S. D. RICE, J. J. PELLA, AND S. G. TAYLOR.
1980. Effects of seeding density of pink salmon, *Oncorhynchus gorbuscha*, eggs on water chemistry, fry characteristics, and fry survival in gravel incubators. Fish. Bull., U.S. 78:649-658.

BAMS, R. A.
1967. Differences in performance of naturally and artificially propagated sockeye salmon migrant fry, as measured with swimming and predation tests. J. Fish. Res. Board Can. 24:1117-1153.
1970. Evaluation of a revised hatchery method tested on pink and chum salmon fry. J. Fish. Res. Board Can. 27:1429-1452.

BURKHALTER, D. E., AND C. M. KAYA.
1977. Effects of prolonged exposure to ammonia on fertilized eggs and sac fry of rainbow trout (*Salmo gairdneri*). Trans. Am. Fish. Soc. 106:470-475.

DOUDOROFF, P., B. G. ANDERSON, G. E. BURDICK, P. S. GALTSOFF, W. B. HART, R. PATRICK, E. R. STRONG, E. W. SURBER, AND W. M. VAN HORN.
1951. Bio-assay methods for the evaluation of acute toxicity of industrial wastes to fish. Sewage Ind. Wastes 23:1380-1397.

EMERSON, K., R. C. RUSSO, R. E. LUND, AND R. V. THURSTON.
1975. Aqueous ammonia equilibrium calculations: effect of pH and temperature. J. Fish. Res. Board Can. 32:2379-2383.

EUROPEAN INLAND FISHERIES ADVISORY COMMISSION.
1970. Water quality criteria for European freshwater fish. Report on ammonia and inland fisheries. FAO, EIFAC (Eur. Inland Fish. Advis. Comm.) Tech. Pap. 11, 12 p.

FINNEY, D. J.
1971. Probit analysis, 3d ed. Camb. Univ. Press, Lond., 333 p.

GARRISON, R. L.
1968. The toxicity of pro-noxfish to salmonid eggs and fry. Prog. Fish-Cult. 30:35-38.

PARKER, R. R.
1971. Size selective predation among juvenile salmonid fishes in a British Columbia inlet. J. Fish. Res. Board Can. 28:1503-1510.

PENAZ, M.
1965. Influence of ammonia on eggs and spawns of stream trout *Salmo trutta* M. Fario. Zool. Listy, Folia Zool. 14:47-53. [Translated by and available from Foreign Fisheries (Translations), U.S. Dep. Commer., Wash., D.C.]

RICE, S. D., AND J. E. BAILEY.
1980. Ammonia concentrations in pink salmon, *Oncorhynchus gorbuscha*, redds of Sashin Creek, southeastern Alaska. Fish. Bull., U.S. 78:809-811.

RICE, S. D., D. A. MOLES, AND J. W. SHORT.
1975. The effect of Prudhoe Bay crude oil on survival and growth of eggs, alevins, and fry of pink salmon, *Oncorhynchus gorbuscha*. *In* Proceedings of 1975 Conference on Prevention and Control of Oil Pollution, p. 503-507. Am. Pet. Inst., Environ. Prot. Agency, and U.S. Coast Guard, Wash., D.C.

RICE, S. D., AND R. M. STOKES.
1975. Acute toxicity of ammonia to several developmental stages of rainbow trout, *Salmo gairdneri*. Fish. Bull., U.S. 73:207-211.

SMART, G. R.
1978. Investigations of the toxic mechanisms of ammonia to fish—gas exchange in rainbow trout (*Salmo gairdneri*) exposed to acutely lethal concentrations. J. Fish. Biol. 12:93-104.

U. S. ENVIRONMENTAL PROTECTION AGENCY.
1974. Methods for chemical analysis of water and wastes. U.S. Environ. Prot. Agency, EPA-625/6-74-003, 298 p.

WURTZ-ARLET, J.
1959. Toxicité des detergents anioniques vis-a-vis des alevins de Truite commune [The toxicity of anionic detergents towards the alevins of common trout]. [In. Fr.] Bull. Fr. Piscic. 32:41-45.

EFFECTS OF SEEDING DENSITY OF PINK SALMON, *ONCORHYNCHUS GORBUSCHA*, EGGS ON WATER CHEMISTRY, FRY CHARACTERISTICS, AND FRY SURVIVAL IN GRAVEL INCUBATORS

JACK E. BAILEY, STANLEY D. RICE, JEROME J. PELLA, AND SIDNEY G. TAYLOR[1]

ABSTRACT

We determined the effects of seeding density of pink salmon eggs in gravel incubators on water chemistry and on size, stage of development, and time of emergence of fry. Sixty days after fertilization, eyed eggs were placed in eight identical test incubators at five different densities (0 to 25,600 eggs per incubator). Test incubators had upwelling water (apparent velocity, 53 cm per hour); 0.015 m^3 of gravel (size, 3-32 mm); and an average incubation temperature of 4.5° C (range, 3.5°-10.0° C). Total ammonia ($NH_3 + NH_4^+$) production and oxygen consumption rates per alevin generally increased throughout incubation. Maximum total ammonia production at any density was about 8×10^{-4} mg/h per alevin. Maximum oxygen consumption was 0.028 mg/h per alevin. The rate of ammonia production and oxygen consumption per alevin increased with increased seeding density until the reduced oxygen concentration limited metabolism. Indications of stress—reduction in size of fry and early emergence—were evident only at the higher seeding densities, 12,800 and 25,600 eggs per 0.015 m^3, and were either absent or unimportant at the lower seeding densities, 1,600 and 6,400 eggs per 0.015 m^3. Un-ionized ammonia (NH_3) concentrations did not reach lethal levels. The stress at higher seeding densities, 12,800 and 25,600 eggs per 0.015 m^3, was probably caused by depletion of oxygen to concentrations below 6 mg/l. Sublethal ammonia concentrations and low dissolved oxygen concentrations were probably synergistic.

Gravel incubators with upwelling water are being tested at hatcheries in the Pacific Northwest for production of fry from eggs of pink salmon, *Oncorhynchus gorbuscha*, chum salmon, *O. keta*, and sockeye salmon, *O. nerka*. To operate most economically, these incubators must be stocked with optimum numbers of eggs and be supplied with a flow of water consistent with production of good quality fry. Frugal use of water is important to hatcheries in Alaska where long, cold winters limit free-flowing water. However, densities of eggs that are too high for water flows result in oxygen depletion or ammonia buildup—stressing conditions that produce undersized fry or early emerging alevins. Both undersized fry and early emerging alevins are believed to survive poorly if released unfed (Bams and Simpson 1977).

Acute ammonia toxicity may not be a significant problem in Alaska where waters typically have low temperature and low pH. Ammonia equilibrates in water to form dissolved, un-ionized NH_3 and ionized NH_4^+ (NH_3 is more toxic than NH_4^+), and low temperature and low pH shift the equilibrium toward NH_4^+ (Emerson et al. 1975). At lower temperatures, however, salmon incubation times are longer than at higher temperatures so that increased cumulative exposure to NH_3 could have adverse effects.

In this paper we describe effects of seeding densities of pink salmon eggs in gravel incubators on 1) oxygen consumption, 2) ammonia production, 3) physical characteristics of fry, 4) survival of fry, and 5) time of volitional emergence. The production limits of the gravel incubators are also defined.

METHODS

Experimental gravel incubators were seeded with different densities of eggs. Temperature, pH, dissolved oxygen, and total ammonia (NH_3 and NH_4^+) concentrations were measured in water entering and leaving the incubators. Rates of oxygen consumption and ammonia production per egg or alevin were estimated during incubation. We monitored numbers and size of fry and time of emergence of fry to identify stressful conditions. Chemical data were compared with biological data to determine maximum seeding densities for the gravel incubators and to define limits of oxygen

[1]Northwest and Alaska Fisheries Center Auke Bay Laboratory, National Marine Fisheries Sevice, NOAA, P.O. Box 155, Auke Bay, AK 99821.

Manuscript accepted January 1980.
FISHERY BULLETIN: VOL. 78, NO. 3, 1980.

and ammonia concentrations that do not produce stressful conditions.

On 16 September 1971, pink salmon eggs were collected from spawners in Sashin Creek on Baranof Island, southeastern Alaska. The eggs were immediately fertilized, water hardened, and placed in Heath[2] trays. On 4 November, we transported the eyed eggs from Sashin Creek to Auke Creek near Juneau, Alaska, and on 16 November, the eggs were placed in eight gravel incubators at five seeding densities—0, 1,600, 6,400, 12,800, and 25,600 eggs/incubator (Table 1).

Each incubator (inside measurements, 30 cm × 30 cm × 30 cm, Bailey and Heard 1973) contained 0.015 m^3 of gravel. A 25 mm layer of bird's-eye gravel (particle size, 2-4 mm) covered the sides and bottom. The remainder of the gravel was larger (particle size, 13-32 mm). We installed airtight covers on the incubators to prevent exchange of gases between atmosphere and water. Water was introduced into each incubator from the bottom in an upwelling flow of 0.8 l/min (apparent velocity, 53 cm/h).

Numbers of eggs were estimated by displacement (Burrows 1951). Precision of the seeding densities, given by ±2 times their estimated standard error (Table 1), was based on appropriate expansion of variation in egg counts from ten 100 ml samples. In previous studies of incubation at this hatchery (Bailey and Taylor 1974), the eggs hatched in late December or early January, 100-120 d after fertilization; and the fry emerged in April, 205-225 d after fertilization. In this study, we expected the eggs to hatch and the fry to emerge at similar times.

Oxygen and total ammonia concentrations were measured weekly between 3 December 1971 and 11 April 1972. Dissolved oxygen concentrations were measured with the Winkler method to the nearest 0.01 mg/l. Total ammonia ($NH_3 + NH_4^+$) in the water was measured with an autoanalyzer using a procedure modified from that of the U.S. Environmental Protection Agency (1974). Our modification used a larger capacity heating bath and measured total ammonia to within 0.004 ppb. If temperature and pH are known, the amount of NH_3 can be calculated from tables by Emerson et al. (1975). When calculating periodic estimates of oxygen uptake and total ammonia production per individual, we corrected for the number of fry that had left the incubator. We assumed the number of alevins in the incubator equaled the final total of alevins emerging from the incubator less the number of alevins already emerged. Temperatures of incubator effluents were measured daily to the nearest 0.1° C, and pH was measured twice a week with a standardized Corning model 112 pH meter. Confidence intervals were calculated for each estimate and displayed graphically. These confidence intervals were computed under the assumptions of normality of variation and homogeneous variance, the latter holding both among incubators and over observation times.

The fry were sampled and counted daily (February through April 1972) as they voluntarily emerged from incubators. Samples of fry were preserved in 5% Formalin for 6 wk. Later we selected three samples of 50 fry from the daily samples of each incubator to represent the days when cumulative fry emergence was 25%, 50%, and 75% of the total emergent fry for each incubator. Fry in these selected samples were measured to the nearest millimeter (fork length) and weighed to the nearest milligram after they were blotted with a damp paper towel. Developmental index (K_D) was computed to determine efficiency of yolk conversion [K_D = 10(weight, milligrams)$^{1/3}$/(length, millimeters), Bams 1972]. The K_D index was computed for unfed fry at the time of emergence. A high K_D indicates a large amount of unabsorbed yolk, whereas a small K_D indicates a small amount of yolk and a more developed fry. The sample of fry at 25% emergence from the incubator seeded with 25,600 eggs was lost.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Survival of pink salmon from eyed egg to migrant fry in gravel incubators seeded with indicated number of eggs (±2 SE).

Eyed eggs per incubator	Survival (%)	Eyed eggs per incubator	Survival (%)
1,600 ± 76	100	6,400 ± 302	92
6,400 ± 302	94	12,800 ± 604	100
6,400 ± 302	92	25,600 ± 1,209	50

TEMPERATURE, pH, AND TOTAL AMMONIA IN INCUBATOR EFFLUENT

Temperature of the water source decreased as the experiment proceeded. Temperature was about 8° C when the eggs were fertilized 16 September 1971 (day 0, Figure 1), remained above 7° C until 14 October (day 28), and then gradually dropped to 3.6° C (range, 3.5°-3.8° C) by 16

FIGURE 1.—Incubation temperature of pink salmon eggs from fertilization, 16 September 1971 (day 0) until termination of the experiment, 28 April 1972 (day 225) after fry emerged from the incubators. Horizontal bars show when eggs hatched and fry emerged from the incubator seeded with 1,600 eggs.

November (day 61). It remained near 3.6° C from 16 November 1971 until termination of the experiment on 28 April 1972 (day 225). The daily temperature variation was <0.2° C.

During the incubation period, pH of the hatchery water supply changed little (pH, 6.13-6.39). Effluents of incubators with eggs had a pH from 6.08 to 6.36. Effluent from the incubator with the highest density of eggs (average pH, 6.19) was more acidic than the hatchery supply (average pH, 6.27).

Concentrations of total ammonia in effluents were higher in seeded incubators than in control incubators and generally increased with more eggs (Figure 2). Concentrations of total ammonia in the effluent from control incubators and in the water supply were nearly identical (maximum concentration about 0.011 mg/l). During the study, maximum concentrations of total ammonia in seeded incubators ranged from 0.03 mg/l for the incubator seeded with 1,600 eggs (March) to 0.32 mg/l for the incubator seeded with 25,600 eggs (January).

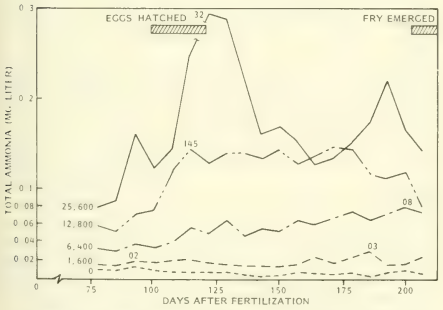


FIGURE 2.—Concentrations of total ammonia in hatchery water supply (0 eggs) and in effluents from incubators seeded with indicated numbers of pink salmon eggs. Horizontal bars show when eggs hatched and fry emerged in the incubator seeded with 1,600 eggs. Peak total ammonia concentration for each seeding density is indicated numerically.

The rate of total ammonia production per individual was periodically measured in all of the incubators. As development progressed from the eyed-egg stage to the emerging fry stage, rate of total ammonia production per individual increased. For example, in the three incubators seeded with 6,400 eggs (Figure 3), the mean of total ammonia production 3 wk before hatching (89 d after fertilization) was $<2 \times 10^{-4}$ mg/h per egg. By hatching (110 d after fertilization), the mean of total ammonia production increased to nearly 4×10^{-4} mg/h per egg. At emergence, approximately 14 wk after hatching (208 d after fertilization), the mean of total ammonia production was almost 6×10^{-4} mg/h per alevin.

The rate of total ammonia production per egg or alevin increased with seeding density (Figure 4). The rates of total ammonia production per individual were meaningless for the incubator with 25,600 eggs (not shown in Figure 4) because many of the eggs and alevins had died and were decomposing and because many of the alevins had emerged 30-60 days early. At the other three seeding densities (1,600, 6,400, and 12,800 eggs), the rates of total ammonia production were higher at higher seeding densities, and the regression of average rates of total ammonia production per indi-

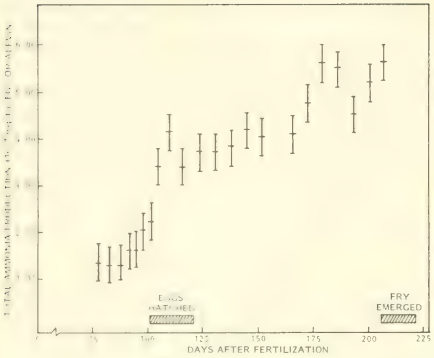


FIGURE 3.—Total ammonia production per individual pink salmon egg or alevin in the three gravel incubators seeded with 6,400 eggs. Ninety-five percent confidence limits for the periodic means were calculated using the error mean square from a one-way ANOVA for sampling periods. Horizontal bars show when eggs hatched and fry emerged.

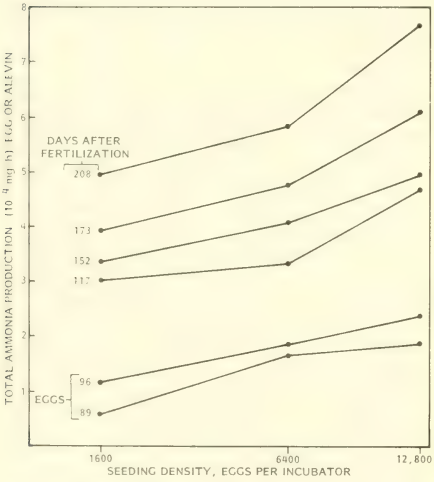


FIGURE 4.—The effect of seeding density on individual ammonia-production rates during development of eggs to emerging alevins. Total ammonia was measured in incubator effluents and was corrected for emergence from the incubators. Eggs hatched 100-120 days after fertilization, and alevins from 1,600-egg density emerged about 203-220 days after fertilization.

vidual egg or alevin in the incubators on their seeding densities was significant ($P<0.01$). The average rate of total ammonia production in each incubator was the mean of 22 periodic rates measured as the eggs developed into emergent fry.

DISSOLVED OXYGEN

Dissolved oxygen concentration in the supply water declined gradually from 9.16 mg/l (70% saturation) on 14 December 1971 (day 89), about 2 wk before the eggs hatched, to 8.08 mg/l (62% saturation) on 11 April 1972 (day 208, Figure 5). This decline was normal because the lake source is usually covered with ice in winter.

Generally, as the eggs developed into fry, dissolved oxygen concentrations in the seeded incubators decreased more in incubators seeded with more eggs (Figure 5), except in the incubator with 25,600 eggs. In the incubator seeded with 25,600 eggs, massive early emergence of fry left fewer alevins in the incubator than in the incubator initially seeded with 12,800 eggs. After the early emergence in the incubator initially seeded with 25,600 eggs, the effluent of the incubator with 12,800 eggs had the lowest dissolved oxygen concentration of the study—3.8 mg/l dissolved oxygen (29% saturated) on 7 March (day 173).

Generally, oxygen consumption per egg or alevin increased steadily during development. At 7-d intervals during incubation, we estimated oxygen consumption rates in each of the three incubators seeded with 6,400 eggs (Figure 6) and averaged these rates. The average rate of oxygen consumption about 2 wk before hatching was about 0.003

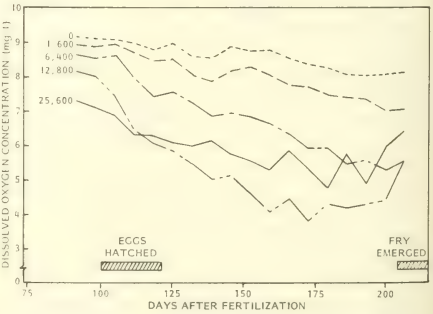


FIGURE 5.—Dissolved oxygen concentration in hatchery water supply (0 eggs) and in effluents from incubators seeded with indicated numbers of pink salmon eggs, December 1971-April 1972. Horizontal bars show when eggs hatched and fry emerged in the incubator seeded with 1,600 eggs.

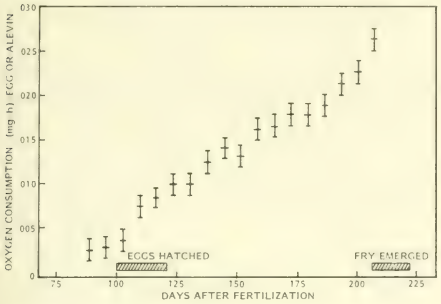


FIGURE 6.—Oxygen consumption per individual pink salmon egg or alevin in three gravel incubators seeded with 6,400 eggs. Ninety-five percent confidence limits for the periodic means were calculated using the error mean square from a one-way ANOVA for sampling periods. Horizontal bars show when eggs hatched and fry emerged.

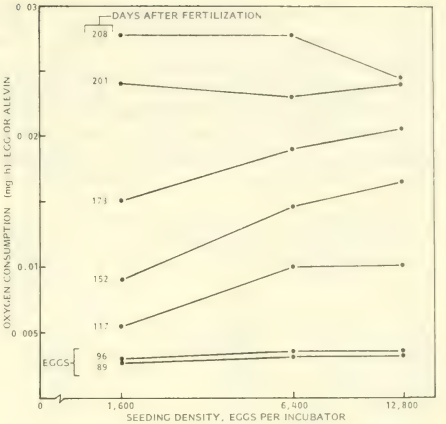


FIGURE 7.—The effect of seeding density on individual oxygen consumption rates during development of eggs to emerging alevins. Oxygen measurements were taken from incubator effluents and corrected for emergence to milligrams/alevin per hour. Eggs hatched 100-120 days after fertilization, and alevins from the 1,600-egg density emerged about 203-220 days after fertilization.

mg/h per egg; by hatching, oxygen consumption increased to about 0.010 mg/h per alevin. The transient peak of oxygen consumption at the end of hatching is probably associated with increases in metabolism due to increases in activity during the hatching process and activity of alevins as they redistribute themselves within the incubator. These transient increases during hatching would have been more significant if the large numbers of eggs in the incubators had hatched synchronously over a day rather than over a 2-wk period. By the time of emergence, oxygen consumption had increased to a mean of 0.027 mg/h per alevin in the incubators seeded with 6,400 eggs. In the incubators seeded with other densities of eggs, oxygen consumption per individual also increased as eggs developed into alevins. The increase in oxygen consumption by eggs and alevins during development was in response to growth and not in response to increased temperature. Temperature remained nearly constant (about 3.6° C) from 2 wk before hatching until all alevins emerged.

Densities of alevins in the incubators influenced the individual oxygen consumption rates (Figure 7). Before hatching, the oxygen consumption rates per egg (days 89 and 96) were about the same in incubators of different densities. After hatching and to the time approaching emergence (days 117, 152, and 173, Figure 7), oxygen demand by individual alevins increased with increased seeding density (excluding the incubator with 25,600 eggs). The incubator seeded with 25,600 eggs (not shown in Figure 7) contained a large number of dead eggs and alevins, which were decomposing. As emergence approached (days 201 and 208), oxygen consumption per alevin did not tend to increase with alevin density.

The increased production of ammonia and consumption of oxygen by alevins with increased seeding densities indicate increased metabolic rates caused by more frequent stimulation and interaction of neighboring alevins.

QUANTITY AND QUALITY OF FRY PRODUCED

Egg-to-Fry Survival and Time of Emergence

Survival from eyed eggs to fry in the incubator seeded with 25,600 eggs (50%) was markedly lower than survival in all other incubators (≥92%, Table 1). Survival was almost 100% in the incubator seeded with 12,800 eggs; the incubator seeded with 12,800 eggs produced almost as many live fry as the incubator seeded with 25,600 eggs. Survival in the incubators seeded with 1,600 eggs and 6,400 eggs ranged from 92% to 100%.

Alevins emerged markedly earlier from incubators seeded with >6,400 eggs (Figure 8). If the

time of 50% emergence in the incubator with 1,600 eggs is used as a standard, 50% of the fry in incubators seeded with 6,400 eggs emerged on the same day (15 April, day 212); 50% of the fry in the incubator seeded with 12,800 eggs emerged 7 d early (8 April, day 205); and 50% of the fry in the incubator seeded with 25,600 eggs emerged 82 d early (24 January, day 130).

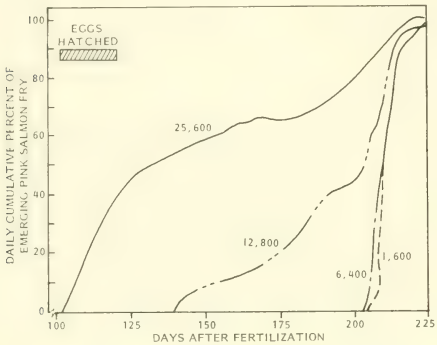


FIGURE 8.—Effect of seeding density on daily cumulative percentages of emergence of pink salmon fry from gravel incubators, December 1971-April 1972. Horizontal bars show when eggs hatched and fry emerged from incubator seeded with 1,600 eggs. Number beside each line is the number of eggs seeded in each incubator.

Size of Fry and Stage of Development

In the incubators with seeding densities above 6,400 eggs, fry emerged earlier and were shorter, lighter, and less developed (higher K_D) than fry in incubators with lower seeding densities.

During the time we monitored emergence, alevins emerging from the incubator seeded with 25,600 eggs were substantially smaller than alevins emerging from the other incubators. At 50% emergence, the alevins in the incubators seeded with 25,600 eggs were in an earlier stage of development (higher K_D) (Figures 9-11) than alevins in other incubators.

Analysis of variance of average lengths of fry at the three lower seeding levels—1,600, 6,400, and 12,800 eggs—indicated significant and changing differences ($P<0.001$), i.e., interaction, in fry length among seeding densities and sampling times (Table 2, Figure 9). At the first sampling time (about 25% emergence), fry emerging from the incubator seeded with 12,800 eggs were substantially smaller than fry emerging from incubators seeded with 1,600 and 6,400 eggs. At the second sampling (about 50% emergence), fry emerging from the incubator seeded with 12,800 eggs were still smaller than fry emerging from incubators seeded with <12,800 eggs, but the difference was not as large as at the first sampling. By the third sampling (about 75% emergence), differences were not statistically significant ($P>0.05$).

Analysis of variance of average weights of the same fry from the three lower seeding densities detected differences among seeding densities (Ta-

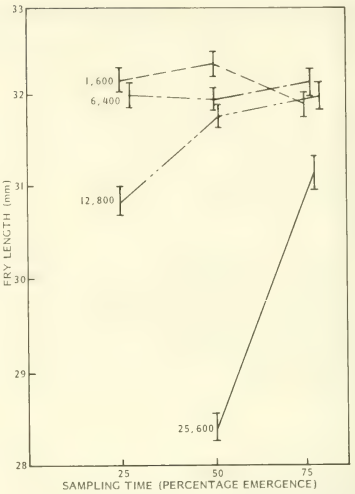


FIGURE 9.—Average length of pink salmon fry that emerged from gravel incubators seeded with indicated numbers of eggs. Samples of 50 fry were taken from each incubator when 25%, 50%, and 75% of emergence from that incubator had occurred. Bars represent 95% confidence limits. The sample for 25% emergence at the 25,600 density was lost.

TABLE 2.—Analysis of variance of average lengths of pink salmon fry, with variation among seeding levels within sampling times partitioned out.

Source	df	SS	MS	F
A Sampling times	2	0.18437	0.09218	—
B Seeding levels	2	0.63706	0.31863	—
Levels in time 1	2	1.21253	0.60626	78.33***
Levels in time 2	2	0.17941	0.08970	11.59**
Levels in time 3	2	0.04821	0.02410	3.11ns
A × B Interaction	4	0.80309	0.20077	25.93***
Within	6	0.04641	0.00774	
Total	14	1.67093		

***$P<0.001$.
**$P<0.01$.
ns = not significant.

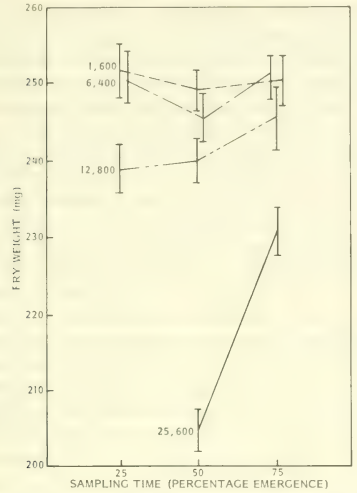


FIGURE 10.—Average weight of pink salmon fry that emerged from gravel incubators seeded with indicated numbers of eggs. Samples of 50 fry were taken from each incubator when 25%, 50%, and 75% of emergence from that incubator had occurred. Bars represent 95% confidence limits. The sample for 25% emergence at the 25,600 density was lost.

ble 3, $P<0.01$). Differences in weights were particularly evident at first sampling (about 25% emergence, Figure 10), although no change in these differences in average weight with time was detectable, i.e., interaction was not significant ($P>0.05$). Mean weight of fry in the incubator seeded with 12,800 eggs was considerably less than the mean weight of fry in the incubators seeded with 1,600 or 6,400 eggs.

Analysis of variance of average developmental index of these fry from incubators seeded with 1,600, 6,400, and 12,800 eggs determined that differences among incubators varied with time, i.e., interaction is significant (Table 4, $P = 0.05$). At the first sampling time, fry from the incubator seeded with 12,800 eggs had a substantially larger mean developmental index (were less developed) than fry from incubators seeded with fewer eggs. Yolk was still visible through the transparent abdominal sutures of fry in the incubator seeded with 12,800 eggs. At the second and third sampling times, developmental indices did not vary significantly among these lower densities ($P>0.05$, Figure 11). However, early-emerging alevins from the incubator seeded with 25,600 eggs were

TABLE 3.—Analysis of variance of average weights of pink salmon fry.

Source	df	SS	MS	F
A Times	2	65.836	32.918	—
B Seeding levels	2	150.0017	75.00085	11.308**
A × B Interactions	4	19.4129	4.853225	0.7317ns
Within	6	39.7934	6.63223	
Total	14	275.0440		

**$P<0.01$.
ns = not significant.

TABLE 4.—Analysis of variance of average developmental index of pink salmon fry with variation among seeding levels within sampling times partitioned out.

Source	df	SS	MS	F
A Sampling times	2	0.00108893	0.000544465	—
B Seeding levels	2	0.00028737	0.000143685	—
Levels in time 1	2	0.00165333	0.000826665	8.24*
Levels in time 2	2	0.00013653	0.000068265	0.68ns
Levels in time 3	2	0.00031413	0.000157065	1.57ns
A × B Interaction	4	0.00181662	0.000454155	4.53*
Within	6	0.00060201	0.000100335	
Total	14	0.00379493		

*$P<0.05$.
ns = not significant.

clearly less developed at the second sampling than early-emerging alevins in the other incubators (Figure 11). (The first sample from the incubator seeded with 25,600 eggs was lost.)

WATER QUALITY AND FRY PRODUCTION IN RELATION TO SEEDING DENSITY

The maximum concentration of total ammonia (0.32 mg/l) detected during the experiment occurred shortly after hatching in the effluent from the incubator seeded with 25,600 eggs. Even in combination with the highest pH encountered during our study (6.4), this total ammonia concentration is equivalent to only 0.092 μg/l NH_3 (0.092 ppb). Concentrations of NH_3 13 times greater (1.2 ppb) inhibit growth of emergent fry after 60-d exposures in their late alevin stages, and concentrations 100 times greater stimulate early emergence of alevins (Rice and Bailey 1980a). Concentrations of $NH_3 \leq 0.4$ ppb have no discernible effect on either size or emergence of the alevins in late stages. Ammonia concentrations in this experiment were not stressing even though alevins nearing emergence are more sensitive to NH_3 than earlier alevin stages (Rice and Stokes 1975; Rice and Bailey 1980a).

Similarly, Rice and Bailey (1980b) did not find toxic concentrations of ammonia in samples of intragravel water taken in late March from a streambed where alevin densities were much

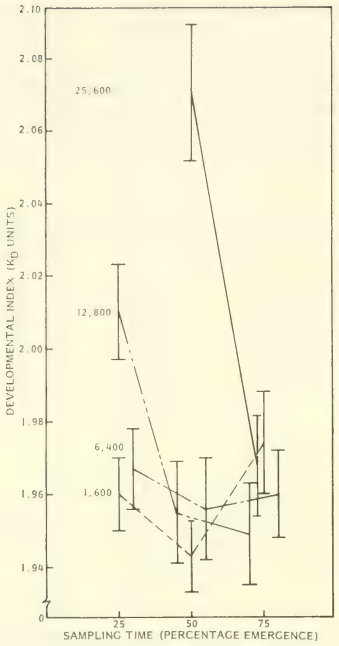


FIGURE 11.—Average developmental indices (Bams 1972) of pink salmon fry that emerged from gravel incubators seeded with indicated numbers of eggs. Samples of 50 fry were taken from each incubator when 25%, 50%, and 75% of emergence from that incubator had occurred. Bars represent 95% confidence limits. The sample for 25% emergence at the 25,600 density was lost.

lower than the highest densities in our experimental incubators. Densities of pink salmon alevins in the stream sampled ranged from 0 to 352 alevins/0.1 m^2 (mean, 21 alevins/0.1 m^2), and the highest concentration of NH_3 was 0.1 ppb. For comparison, the alevin densities in our experiment were >1,700 alevins/0.1 m^2.

Oxygen consumption rates per individual increased with time. The highest rate observed (0.028 mg/h per alevin) occurred near the end of incubation when 25% of the fry had emerged from the incubators seeded with 1,600 and 6,400 eggs. Further increases in rate of oxygen consumption per alevin might have occurred before emergence was complete, but this potential for stress was eliminated because fry left the incubators.

The respiration rates of salmon eggs and alevins are oxygen dependent (Fry 1957); consequently, low dissolved oxygen concentrations in the water will limit normal metabolic rates. Our data suggest that oxygen concentrations below about 6 mg/l may decrease the normal metabolism of pink salmon alevins, although survival to emergence may not be noticeably affected. Alevins in the incubator seeded with 12,800 eggs were probably stressed and began to emerge early, about 60 d earlier than alevins in lower density incubators (Figure 8), when oxygen concentrations decreased to about 5 mg/l (Figure 5). Just prior to peak emergence (201 and 208 d after fertilization), alevins in the incubators seeded with 6,400 and 12,800 eggs probably had their oxygen consumption limited because oxygen concentrations had decreased to <6 mg/l at a time when their demand was greatest. If oxygen concentrations were not limiting, oxygen consumption rates (Figure 7) would have been greater than the rates for alevins in the 1,600-egg incubator as in the earlier measurements.

Although ammonia (NH_3) alone did not increase to concentrations that decreased size at emergence or reduced survival, it may have acted synergistically with relatively low oxygen concentrations to create stressful conditions in our study. In earlier studies, survival time of fish exposed to ammonia (NH_3) was reduced at adequate but low oxygen levels (Wuhrmann 1952; Downing and Merkens 1955).

Stressful conditions associated with low dissolved oxygen concentrations alone, or in combination with ammonia, probably not only reduced survival and caused premature emergence of fry but may have also reduced the ability of alevins to use yolk for growth. In incubation studies at similar temperatures, the developmental indices decreased and lengths increased just before emergence of pink salmon fry (Bams 1972; Bailey and Taylor 1974). A decrease of 0.01 in K_D corresponds to about 0.2 mm increase in length (Bams 1972; Bailey and Taylor 1974). In our study, the developmental index decreased to about 1.96 at emergence in the incubator seeded with 1,600 eggs (Figure 11). The fry in the incubator seeded with 25,600 eggs were 28.44 mm, mean length, at 50% emergence and had a mean developmental index of 2.07. If these fry had remained in the incubator until their developmental index decreased to 1.96, they would have been only 30.64 mm long, 1.52 mm shorter than the fry emerging from the incubator seeded with 1,600 eggs.

Survival from egg to fry exceeded 90% in in-

cubators seeded with <25,600 eggs, but survival was only 50% in the incubator seeded with 25,600 eggs. We attribute this poor survival to crowding, possibly low dissolved oxygen concentrations, or the combined effects of these and elevated NH_3 concentrations. Ammonia, as a single factor, is unlikely to reach levels harmful to pink salmon alevins in gravel incubators supplied with slightly acidic water, as the water in Auke Creek. However, if the pH were 7.75 rather than 6.4, then the highest concentration of total ammonia, 0.32 mg/l, would be equivalent to 2.1 ppb of NH_3 and would reduce survival.

Much remains to be learned before we can define combinations of seeding density and water flow for efficient production of healthy, unfed fry. Seeding densities of 1,200-1,800 eggs/0.015 m^3 of gravel and an apparent water velocity of 70-300 cm^3/h per cm^2 can be used (Bams 1972; Bailey et al. 1976). Bams and Simpson (1977) suggested that 1,965 eggs/0.015 m^3 with a water velocity of 200 cm/h is safe. In our study, increasing seeding density from 1,600 eggs/0.015 m^3 to 6,400 eggs/0.015 m^3 at a water flow of 53 cm/h apparently increased swimming activity of the alevins and also increased oxygen consumption and ammonia production. However, the average length, weight, developmental index, emergence time, and survival of these alevins were not importantly affected.

Under our experimental conditions, a seeding density of 6,400 eggs/0.015 m^3 appears to be acceptable, although perhaps a nearly maximum seeding density. Our test incubators were operated at a water flow of only 0.8 l/min (apparent velocity, 53 cm^3/h per cm^2). If an apparent water velocity of 200 cm^3/h per cm^2 were used as recommended by Bams and Simpson (1977), acceptable seeding densities might be higher.

SUMMARY

Pink salmon eggs were seeded in gravel incubators at four different densities (from 1,600 to 25,600 eggs/0.015 m^3 of gravel) and incubated until fry voluntarily emerged. Dissolved oxygen and total ammonia concentrations of the incubator effluent were monitored periodically, and the emerged fry were counted, sampled, and measured. The rate of total ammonia production per egg or alevin increased with time after seeding at all densities. At seeding densities of 6,400 eggs/0.015 m^3 the rate of total ammonia production increased from 2×10^{-4} mg/h per egg 3 wk before hatching, to 4×10^{-4} mg/h per alevin at hatching, to 6×10^{-4} mg/h per alevin at emergence. The rate of total ammonia production per individual also increased with seeding density. Because of low pH and low temperature, NH_3 concentrations did not reach toxic or lethal concentrations in any incubator; however, NH_3 concentrations would have become toxic in the incubator seeded with the most eggs (25,600 eggs/0.015 m^3) shortly after hatching if the pH had been 7.75 rather than 6.4.

Rate of oxygen consumption per egg or alevin increased during incubation. In the incubator seeded with 6,400 eggs/0.015 m^3, it increased from 0.003 mg/h per egg 3 wk before hatching, to 0.007 mg/h per egg at hatching, to 0.028 mg/h per alevin at emergence. Probably because of increased interaction between adjacent alevins, rates of oxygen consumption per hour per alevin increased, until emergence, with increased seeding density. In incubators seeded with >6,400 eggs/0.015 m^3, dissolved oxygen concentrations dropped to stressful levels (<6 mg/l) that limited metabolism. At seeding densities >6,400 eggs/0.015 m^3, stressful conditions caused early emergence of premature fry and reduced the ability of alevins to convert yolk for growth. Additionally, survival was reduced at 25,600 eggs/0.015 m^3. At an apparent water velocity of 53 cm^3/h per cm^2, a seeding density of 6,400 eggs appeared to be marginally acceptable for the production of healthy pink salmon fry.

ACKNOWLEDGMENTS

The pH determinations were made by James Knull, oceanographer at the Auke Bay Laboratory. We wish to thank Don Alderdice, Environment Canada, for his helpful review of this manuscript.

LITERATURE CITED

BAILEY, J. E., AND W. R. HEARD.
1973. An improved incubator for salmonids and results of preliminary tests of its use. U.S. Dep. Commer., NOAA Tech. Memo. NMFS ABFL-1, 7 p.

BAILEY, J. E., J. J. PELLA, AND S. G. TAYLOR.
1976. Production of fry and adults of the 1972 brood of pink salmon, *Oncorhynchus gorbuscha*, from gravel incubators and natural spawning at Auke Creek, Alaska. Fish. Bull., U.S. 74:961-971.

BAILEY, J. E., AND S. G. TAYLOR.
1974. Salmon fry production in a gravel incubator hatchery, Auke Creek, Alaska, 1971-72. U.S. Dep. Commer., NOAA Tech. Memo. NMFS ABFL-3, 13 p.

BAMS, R. A.
1972. A quantitative evaluation of survival to the adult stage and other characteristics of pink salmon (*Oncorhynchus gorbuscha*) produced by a revised hatchery method which simulates optimal natural conditions. J. Fish. Res. Board Can. 29:1151-1167.

BAMS, R. A., AND K. S. SIMPSON.
1977. Substrate incubators workshop - 1976. Report on current state-of-the-art. Environ. Can., Fish. Mar. Serv., Tech. Rep. 689, 68 p.

BURROWS, R. E.
1951. A method for enumeration of salmon and trout eggs by displacement. Prog. Fish-Cult. 13:25-30.

DOWNING, K. M., AND J. C. MERKENS.
1955. The influence of dissolved-oxygen concentration on the toxicity of un-ionized ammonia to rainbow trout (*Salmo gairdnerii* Richardson). Ann. Appl. Biol. 43:243-246.

EMERSON, K., R. C. RUSSO, R. E. LUND, AND R. V. THURSTON.
1975. Aqueous ammonia equilibrium calculations: effect of pH and temperature. J. Fish. Res. Board Can. 32:2379-2383.

FRY, F. E. J.
1957. The aquatic respiration of fish. *In* M. E. Brown (editor), The physiology of fishes. Vol. I, p. 1-63. Acad. Press, N.Y.

RICE, S. D., AND J. E. BAILEY.
1980a. Survival, size, and emergence of pink salmon, *Oncorhynchus gorbuscha*, alevins after short- and long-term exposures to ammonia. Fish. Bull., U.S. 78:641-648.
1980b. Ammonia concentrations in pink salmon, *Oncorhynchus gorbuscha*, redds of Sashin Creek, southeastern Alaska. Fish. Bull., U.S. 78:809-811.

RICE, S. D., AND R. M. STOKES.
1975. Acute toxicity of ammonia to several developmental stages of rainbow trout, *Salmo gairdneri*. Fish. Bull., U.S. 73:207-211.

U.S. ENVIRONMENTAL PROTECTION AGENCY.
1974. Methods for chemical analysis of water and wastes. U.S. Environ. Prot. Agency, EPA-625-16-74-003, 298 p., Wash., D.C.

WUHRMANN, K.
1952. Sur quelques principes de la toxicologie du poisson. Bull. Cent. Belge Etud. Doc. Eaux 15:49.

SOME STATISTICAL CONSIDERATIONS OF THE DESIGN OF TRAWL SURVEYS FOR ROCKFISH (SCORPAENIDAE)

WILLIAM H. LENARZ AND PETER B. ADAMS[1]

ABSTRACT

This study is in two parts. The first part reviews statistical theory for choosing among random, stratified random, and systematic sample survey schemes when strata are of equal size and receive equal sampling effort. The theory is applied to data collected during a pilot trawl survey for rockfish in Queen Charlotte Sound, British Columbia, and a full scale survey along the coasts of Washington, Oregon, and California. The results indicate that on a scale of about 80 km, a systematic survey scheme provides more precise estimates than the other schemes. However, the differences in precision are slight and probably should not outweigh other factors such as logistical constraints in the design of trawl surveys. The second part of the study reviews statistical theory for sampling from negative binomial distributions. Results of the Queen Charlotte Sound pilot survey indicate that except for fish with very low densities, numerous tows of short distances are relatively more precise than fewer tows of longer distances for trawl surveys for rockfish.

The Fisheries Conservation and Management Act of 1976 requires the development of fishery management plans for each marine fishery under jurisdiction of the United States. The requirement emphasizes the need to assess the status of U.S. fisheries. Estimates of stock abundance are essential for fishery assessment, and trawl surveys often are used to estimate absolute or relative stock abundance where suitable data from a fishery itself are lacking.

Very little data are available from the complex fisheries for rockfish (genus *Sebastes*) of the Pacific coast of North America. The fisheries are complex because many species and types of gear are involved. Often landing statistics do not specify species, and catches are seldom sufficiently sampled for age, length, and sex composition. Catch per effort data also are not reported by species and are difficult to interpret because of temporal changes in fishing power and target species.

Because of this lack of needed data, the Northwest and Alaska Fisheries Center of the National Marine Fisheries Service initiated a large scale trawl survey of rockfish stocks from southern California to the Aleutian Islands. The first stage of the 4-yr survey was to conduct pilot surveys in the Monterey Bay area, Calif., and Queen Charlotte Sound, British Columbia, during 1976. The overall goal of the pilot surveys was to provide information for design of the full scale survey. Gunderson and Nelson[2] describe the pilot survey and present preliminary results of the effort. A full scale survey was conducted in 1977 off the coasts of Washington, Oregon, and California. Design of the 1977 survey was partly based on results of the pilot surveys. Gunderson and Sample (1980) discussed the 1977 survey.

While trawl surveys have proven to be a useful tool for assessing fish stocks, problems still remain in their design and analysis. This paper presents analyses of results of the Queen Charlotte Sound pilot survey and 1977 survey. The analyses were aimed at answering three questions: 1) Should the full scale survey design be based on a random, stratified random, or systematic scheme? 2) Do results of the 1977 survey indicate that aspects of the design based on the pilot survey were correct? 3) What are the trade offs in precision between distance trawled and number of tows? Ancillary to question one are the questions: 1) Are there significant benefits to be gained by choosing one or a combination of the three sampling schemes? 2) Are there significant biases in estimates of

[1]Southwest Fisheries Center Tiburon Laboratory, National Marine Fisheries Service, NOAA, 3150 Paradise Drive, Tiburon, CA 94920.

[2]Gunderson, D. R., and M. O. Nelson. 1977. Preliminary report on an experimental rockfish survey conducted off Monterey, California and in Queen Charlotte Sound, British Columbia during August-September, 1976. Prepared for February 15-16, 1977 Interagency Rockfish Survey Coordinating Committee Meeting, Northwest and Alaska Fisheries Center, Seattle, Wash., 82 p.

Manuscript accepted December 1979.
FISHERY BULLETIN: VOL. 78, NO. 3, 1980.

either means or variances using one or a combination of the three sampling schemes?

While our analyses are limited to data from the Queen Charlotte Sound pilot survey and the 1977 survey, the questions repeatedly arise in discussions of trawl surveys and thus are of general interest.

COMPARISONS OF RANDOM, STRATIFIED RANDOM, AND SYSTEMATIC SAMPLING

Methodology

Chapter 8 of Cochran (1964) discusses systematic sampling and presents methodology for choosing among random, stratified random, and systematic (every kth) sampling. Similar discussions are found in other sampling texts such as Hansen et al. (1953) and Sukhatme and Sukhatme (1970). The methodology used in comparing the three sampling techniques assumes equal sampling effort in each strata. If prior information indicated that variance differs considerably among strata, the optimal stratified random sampling scheme would not be equal allocation of sampling effort among strata. Unfortunately as shown by Abramson (1968), it can be difficult to obtain meaningful information on within strata variance for trawl surveys even if previous surveys have been made in the area. The methodology also only considers regularly spaced strata of uniform size. While prior knowledge (catch records) made it possible to design strata of unequal size on a large scale basis, knowledge is insufficient to do so on the scale considered in the analysis. The multispecies aspects of the survey made it particularly difficult to devise an optimal stratified random scheme.

In this section we use Cochran's notation. However, instead of examining components of variance for choosing among the three types of sampling as Cochran did, we calculated the variances for each type of sampling. Using the notation of Cochran, let a population of k possible systematic samples be represented by

Member	*Systematic sample number*				
	1	...	i	...	k
1	y_{11}	...	y_{i1}	...	y_{k1}
.	.		.		.
.	.		.		.
.	.		.		.
j	y_{1j}	...	y_{ij}	...	y_{kj}
.	.		.		.
.	.		.		.
.	.		.		.
n	y_{1n}	...	y_{in}	...	y_{kn}

where y_{ij} is the jth member of the ith systematic sample.

If the y_{ij}'s are arranged as they actually occur for a population of two systematic samples ($k = 2$) with four ($n = 4$) members they appear as follows:

Unit	1	2	3	4	5	6	7	8
Variable	y_{11}	y_{21}	y_{12}	y_{22}	y_{13}	y_{23}	y_{14}	y_{24}.

In a systematic survey a number (i) is chosen between 1 and k and then n members that are k units apart are sampled. Under a scheme of drawing one systematic sample, either units 1, 3, 5, and 7 or 2, 4, 6, and 8 would be observed. Under a stratified random scheme one unit out of each of four strata (units 1 and 2, 3 and 4, 5 and 6, and 7 and 8) would be chosen at random for observation. Under the corresponding random scheme any four of the eight units would be chosen at random to be observed. The example population contains 2 possible systematic samples, 16 possible stratified random samples, and 70 possible random samples. While more than 20% of the possible random samples match with a stratified random sample, <3% match with a systematic sample. A systematic sample is much more structured or constrained than the other schemes. Population variances of the means of random, stratified random, and systematic sampling are calculated as follows:

$$V(\bar{y}_{ran}) = \frac{N-n}{N} \; S^2_{ran}/n \qquad (1)$$

where $V(\bar{y}_{ran})$ = variance of the mean calculated from random sampling ($\bar{y}_{ran}$),

$$N = k \times n,$$

$$S^2_{ran} = \sum_{i=1}^{k} \sum_{j=1}^{n} (y_{ij} - \bar{y})^2 / N-1,$$

$$\bar{y} = \sum_{i=1}^{k} \sum_{j=1}^{n} y_{ij} / N,$$

$$V(\bar{y}_{st}) = \frac{(N-n)}{N} S_{st}^2/n \qquad (2)$$

where $V(\bar{y}_{st})$ = variance of the mean calculated from stratified random sampling ($\bar{y}_{st}$),

$$S_{st}^2 = \frac{1}{n(k-1)} \sum_{j=1}^{n} \sum_{i=1}^{k} (y_{ij} - \bar{y}_{.j})^2,$$

$$\bar{y}_{.j} = \sum_{i=1}^{k} y_{ij}/k, \text{ and}$$

$$V(\bar{y}_{sys}) = \frac{1}{k} \sum_{i=1}^{k} (\bar{y}_{i.} - \bar{y})^2 \qquad (3)$$

where $V(\bar{y}_{sys})$ = variance of the mean calculated from systematic sampling ($\bar{y}_{sys}$),

$$\bar{y}_{i.} = \sum_{j-1}^{n} y_{ij}/n.$$

If k systematic samples are taken from a population that is sufficiently large to ignore the finite population correction factor then the variance estimates become:

$$S^2(\bar{y}_{ran}) = S_{ran}^2/n \qquad (4)$$

where $S^2(\bar{y}_{ran})$ = estimate of $V(\bar{y}_{ran})$,

$$S_{ran}^2 = \sum_{i=1}^{k} \sum_{j=1}^{n} (y_{ij} - \bar{y})^2/(nk-1),$$

$$\bar{y} = \sum_{i=1}^{k} \sum_{j=1}^{n} y_{ij}/kn,$$

$$S^2(\bar{y}_{st}) = S_{st}^2/n \qquad (5)$$

where $S^2(\bar{y}_{st})$ = estimate of $V(\bar{y}_{st})$,

$$S_{st}^2 = \frac{1}{n(k-1)} \sum_{j=1}^{n} \sum_{i=1}^{k} (y_{ij} - \bar{y}_{.j})^2,$$

$$y_{.j} = \sum_{i=1}^{k} y_{ij}/k, \text{ and}$$

$$S^2(\bar{y}_{sys}) = \frac{1}{k-1} \sum_{i=1}^{k} (\bar{y}_{i.} - y)^2 \qquad (6)$$

where $S^2(\bar{y}_{sys})$ = estimate of $V(\bar{y}_{sys})$,

$$\bar{y}_{i.} = \sum_{j=1}^{n} y_{ij}/n.$$

Results of Pilot Survey

In the case of the Queen Charlotte survey, two random starting points were chosen and then tows were made along four transects for each of the two systematic samples. The transects within a systematic sample were approximately 16.1 km (10 mi) apart and bottom topography dictated some deviations from the desired transects. Because preferred depths differ among species of rockfish (e.g., *Sebastes alutus* is relatively scarce in shallow waters, while *S. proriger* is relatively scarce in deep waters), attempts were made to distribute sampling effort among 18.3 m (10-fathom) depth intervals within the depth range of concern, 91.4 m (50 fathoms) and 292 m (160 fathoms). Examination of the data indicated that, to obtain reasonable sample sizes, observations should be divided into only three depth intervals: 91-145 m (79 fathoms), 146-181 m (80-99 fathoms), and >181 m.

The Queen Charlotte data were organized in two ways to examine the relative precision of the three sample schemes. We first arranged tows at depths >181 m into a hypothetical population of four systematic samples for each species. While the original sample design called for two systematic samples, the two random starting points resulted in all transects being about 8.1 km (5 mi) apart. Each systematic sample contains two members. Furthermore, each hypothetical population is composed of x_{is} = the average catch (kilograms) per 1.8 km (nautical mile) of species s of all tows taken >181 m in transect i of the Queen Charlotte survey. Under the preceding definition the hypothetical population of systematic samples of species s is

Member	*Systematic sample*			
	1	2	3	4
1	$y_{11} = X_{1s}$	$y_{21} = X_{2s}$	$y_{31} = X_{3s}$	$y_{41} = X_{4s}$
2	$y_{12} = X_{5s}$	$y_{22} = X_{6s}$	$y_{32} = X_{7s}$	$y_{42} = X_{8s}$.

In this case $k = 4$ and $n = 2$. The y_{ij}'s are averages of 1-5 tows (Table 1). The resulting estimates of variance apply only to these hypothetical populations and particular mixture of tows per average (y_{ij}). It was not possible to construct similar hypothetical populations for the other depth intervals because of missing cells.

Values of V ($\bar{y}_{ran}$), V ($\bar{y}_{st}$), and V ($\bar{y}_{sys}$) for the first hypothetical populations are shown in Table 2. Comparison of the precision of the three sampling methods indicates that systematic sampling would be the most precise (has lowest variance) scheme for 8 of the 15 species. Ties occurred for the other seven species. Assuming that each species represents an independent observation, the sign test indicated that systematic sampling gave better results than stratified random sampling and random sampling at the 1% level of significance, and that stratified random sampling did not give significantly better results than random sampling.

Because of the uneven distribution of tows per transect, we organized the data in another fashion to determine if the relative precision of the three sampling schemes is affected by organization of the data.

We next grouped the data into three depth intervals: 91-145 m, 146-181 m, and >181 m. In order to avoid missing cells it was necessary to create hypothetical populations of only two systematic samples with two members. We did so as follows: X_{isd} = the average of catch (kilograms) per 1.8 km of species s in depth interval d of all tows in transects i and $i+1$. The hypothetical population of systematic samples of species s from depth interval d is

Member (stratum)	*Systematic sample*	
	1	2
1	$y_{11} = X_{1 \text{ and } 2.\ s.\ d}$	$y_{21} = X_{3 \text{ and } 4.\ s.\ d}$
2	$y_{12} = X_{5 \text{ and } 6.\ s.\ d}$	$y_{22} = X_{7 \text{ and } 8.\ s.\ d}$.

In this case $k = 2$ and $n = 2$. The y_{ij}'s are averages of 1 to 9 tows (Table 1). The values of V ($\bar{y}_{ran}$), V ($\bar{y}_{st}$), and V ($\bar{y}_{sys}$) are shown in Table 3.

The results indicate that systematic sampling produces more precise estimates of rockfish densities than either random or stratified random sampling. However, the sign test revealed that systematic sampling is not significantly better than stratified random sampling and only better than random sampling at the 5% level of significance. Stratified random sampling was not significantly better than random sampling. While systematic sampling appears to be the most precise of the three survey design schemes, there were many cases in which two or more of the schemes would be equally precise. In many other cases little precision would be lost if either stratified random or random designs were chosen.

TABLE 1.—Number of tows taken during the Queen Charlotte survey by stratum, systematic sample, member, and group of hypothetical populations.

First group of hypothetical populations Systematic sample				
Member	1	2	3	4
1	1	1	1	2
2	2	2	4	5

Second group of hypothetical populations Systematic sample			
Depth (m)	Member	1	2
91-145	1	2	8
	2	6	2
146-181	1	6	5
	2	2	1
>181	1	2	3
	2	4	9

TABLE 2.—Variances of means of catch (per 1.8 km towed) from the first hypothetical populations of Queen Charlotte rockfish. Calculations are made under random, stratified random, and systematic sampling schemes.

	Variance		
Population	Random	Stratified random	Systematic
Sebastes alutus	6,595.069	5,791.227	3,312.254
S. flavidus	0.188	0.188	0.188
S. pinniger	0.003	0.003	0.003
S. paucispinis	0.766	0.734	0.620
S. brevispinis	6.601	6.431	6.273
S. elongatus	0.002	0.002	0.002
S. proriger	0.002	0.002	0.002
S. babcocki	225.734	238.282	191.356
S. crameri	0.107	0.083	0.060
S. zacentrus	73.723	74.613	71.624
S. diploproa	0.344	0.329	0.329
S. entomelas	0.117	0.117	0.117
S. reedi	74.625	74.625	74.625
S. aleutianus	0.246	0.266	0.163
S. helvomaculatus	0.056	0.057	0.054

Results of 1977 Survey

The 1977 survey design included both stratified random and systematic sampling strategies. The coast was stratified into three types of areas: high density sampling, low density sampling, and no

TABLE 3.—Variances of means of catch (per 1.8 km towed) from second hypothetical populations of Queen Charlotte rockfish. Calculations are made under random, stratified random, and systematic sampling schemes.

Population	Depth interval (m)	Variance		
		Random	Stratified random	Systematic
Sebastes alutus	91-145	82.313	59.446	55.285
S. alutus	146-181	2,745.670	3,803.277	1,125.770
S. alutus	>181	1,892.520	1,270.058	2,502.014
S. flavidus	91-145	8.442	12.750	0.102
S. flavidus	146-181	0.259	0.193	0.160
S. flavidus	>181	0.063	0.063	0.063
S. pinniger	91-145	257.220	234.198	228.577
S. pinniger	146-181	0.507	0.759	0.400
S. pinniger	>181	0.001	0.001	0.001
S. paucispinis	91-145	2.657	3.987	1.503
S. paucispinis	146-181	1.560	0.287	0.402
S. paucispinis	>181	0.260	0.197	0.121
S. brevispinis	91-145	60.440	19.718	13.783
S. brevispinis	146-181	8.703	13.020	11.262
S. brevispinis	>181	2.328	2.194	3.464
S. elongatus	91-145	0.129	0.100	0.102
S. elongatus	146-181	0.327	0.317	0.345
S. elongatus	>181	0.001	0.001	0.001
S. proriger	91-145	1,019.197	686.814	657.281
S. proriger	146-181	5.152	5.560	6.494
S. proriger	>181	0.002	0.002	0.002
S. babcocki	91-145	2.090	1.584	1.169
S. babcocki	146-181	3.241	0.339	0.339
S. babcocki	>181	49.730	50.671	24.671
S. crameri	91-145	0.001	0.001	0.001
S. crameri	146-181	0.057	0.051	0.029
S. crameri	>181	0.061	0.037	0.074
S. zacentrus	91-145	0.006	0.006	0.006
S. zacentrus	146-181	0.220	0.217	0.217
S. zacentrus	>181	29.261	30.641	30.641
S. diploproa	91-145	0.000	0.000	0.000
S. diploproa	146-181	0.000	0.000	0.000
S. diploproa	>181	0.165	0.162	0.162
S. entomelas	91-145	0.006	0.006	0.006
S. entomelas	146-181	0.609	0.724	0.378
S. entomelas	>181	0.048	0.048	0.048
S. reedi	91-145	0.000	0.000	0.000
S. reedi	146-181	0.302	0.302	0.302
S. reedi	>181	30.710	30.710	30.710
S. aleutianus	91-145	0.000	0.000	0.000
S. aleutianus	146-181	0.002	0.002	0.002
S. aleutianus	>181	0.087	0.057	0.018
S. helvomaculatus	91-145	0.000	0.000	0.000
S. helvomaculatus	146-181	0.001	0.001	0.001
S. helvomaculatus	>181	0.022	0.024	0.020

sampling. Areas in which historical fisheries data indicated high abundances of important rockfish species were assigned high density sampling. In these areas, transects were set at 8.1 km (5-mi) intervals. The typical high density area used in the study was about 81 km (50 mi) long. Transects in other areas were set at 16.1 km (10-mi) intervals unless bottom topography precluded sampling. Each transect was divided into four 91 m (50-fathom) depth strata between 91 and 457 m (250 fathoms). Sampled depths were then chosen at random within each depth stratum of a transect. The number of samples within a depth stratum was proportional to the bottom area of that stratum.

The survey design was based on several factors. The large scale stratification along the coast was an attempt to make sampling proportional to expected densities of important rockfish. This was done with the knowledge that there often are positive correlations among means and variances of fish densities. Depths were randomly chosen because it was known that often within an area densities of many species of rockfish sometimes only occur over a narrow depth interval. Thus, unless depths were chosen at random, bias could occur. Sampling was proportional to bottom area, because bottom area is used to convert fish densities to abundance estimates. Systematic transects were taken to ensure adequate aerial coverage for one intended use of the data, because of logistics and the results of the pilot survey.

Four high density areas had sufficient sampling effort to be included in the study. Eight or more adjacent transects were sampled in one or more depth strata in each chosen area. Area 1 was between lat. 34°33′ and 35°19′ N, area 2: lat. 35°19′ and 35°59′ N, area 3: lat. 39°7′ and 39°53′ N, and area 4: lat. 44°59′ and 45°50′ N. If more than one sample was taken from a depth stratum of a transect, one sample was chosen at random for the study. As in the case of the first Queen Charlotte hypothetical populations, populations of four or five systematic samples of two members each were created from the data. The results again indicated that systematic samples were slightly more precise than either random or stratified random (Table 4). The sign test indicated that systematic sampling was more precise than random at the 1% level of significance and stratified random at the 10% level. Stratified random sampling was not significantly less precise than random.

The data were also arranged into two systematic samples with four or five members each. Systematic sampling was more precise than random at the 1% level of significance, but was not significantly more precise than stratified random (Table 5). Stratified random sampling was not significantly less precise than random sampling.

Discussion

The results of this study indicate that on a scale of about 80 km along the coast systematic sampling for rockfish is slightly more precise than random sampling or a stratified random scheme with regularly spaced strata of equal size and

TABLE 4.—Variances of means of catch (per 1.8 km towed) from hypothetical populations of rockfish that were constructed from 1977 survey data. Calculations are made under random, stratified random, and systematic sampling schemes. Hypothetical populations are composed of either four or five systematic samples with two members.

Population	Systematic samples	Area	Depth interval (m)	Variance		
				Random	Stratified random	Systematic
Sebastes alutus	4	4	183-273	6,276.924	6,232.073	5,426.781
S. alutus	4	4	366-457	46.552	49.621	51.403
S. flavidus	4	2	91-182	0.090	0.102	0.074
S. pinniger	4	1	91-182	8.420	6.604	6.604
S. pinniger	4	2	91-182	0.185	0.215	0.422
S. paucispinis	4	1	91-182	9,630.529	9,888.812	8,989.353
S. paucispinis	4	2	91-182	34.452	39.381	27.818
S. paucispinis	5	2	183-273	24.181	23.665	30.904
S. paucispinis	5	3	91-182	37.490	42.176	81.772
S. brevispinis	4	4	183-273	2.185	2.290	1.421
S. elongatus	4	1	91-182	3.651	3.930	3.039
S. elongatus	4	2	183-273	0.060	0.054	0.054
S. elongatus	5	3	91-182	3.062	2.994	2.994
S. elongatus	4	4	183-273	63.100	66.665	93.148
S. babcocki	4	2	183-273	3.974	3.434	3.434
S. babcocki	4	2	274-365	4.998	5.820	8.106
S. babcocki	4	3	366-457	0.789	0.469	0.469
S. babcocki	4	4	183-273	7.761	6.086	6.125
S. babcocki	4	4	366-457	90.164	85.971	85.971
S. crameri	4	2	274-365	32.481	27.882	26.134
S. crameri	5	2	366-457	3.516	3.200	3.200
S. crameri	4	4	183-273	1,903.722	1,948.233	1,741.187
S. crameri	4	4	366-457	0.230	0.251	0.110
S. zacentrus	4	4	183-273	15.078	12.492	12.492
S. diploproa	4	2	183-273	1,255.342	1,389.344	1,317.551
S. diploproa	4	2	274-365	2,861.498	3,304.897	5,275.483
S. diploproa	5	2	366-457	2,727.360	1,979.702	948.597
S. diploproa	4	3	366-457	159.021	68.670	91.114
S. diploproa	4	4	183-273	683.478	700.234	779.467
S. diploproa	4	4	366-457	1.827	1.966	1.216
S. entomelas	4	1	91-182	467.709	468.780	476.280
S. entomelas	4	2	91-182	1.012	1.001	0.981
S. entomelas	4	2	183-273	3.050	3.103	2.633
S. entomelas	5	3	91-182	0.376	0.423	0.846
S. entomelas	4	4	183-273	3.002	3.057	2.129
S. aleutianus	4	4	366-457	589.997	688.030	399.129
S. goodei	4	1	91-182	119.235	119.105	121.329
S. goodei	4	2	91-182	4,439.160	4,391.472	4,226.895
S. goodei	4	2	183-273	416.868	468.696	301.373
S. goodei	5	3	91-182	258.380	221.057	220.347
S. jordani	4	1	91-182	467.621	406.738	399.790
S. jordani	4	2	91-182	26,765.442	27,254.716	25,958.703
S. jordani	4	2	183-273	7.256	8.158	5.457
S. jordani	5	3	91-182	0.575	0.570	0.570
S. saxicola	4	1	91-182	11,033.375	8,981.548	8,450.645
S. saxicola	4	2	91-182	145.957	162.133	120.545
S. saxicola	4	2	183-273	11,177.436	11,261.334	11,301.092
S. saxicola	4	2	274-365	0.244	0.235	0.235
S. saxicola	5	2	366-457	0.104	0.066	0.057
S. saxicola	5	3	91-182	3,402.868	3,070.065	3,068.507
S. saxicola	4	3	366-457	3.106	3.304	2.843
S. saxicola	4	4	183-273	4.630	4.187	3.308
S. rufus	4	2	183-273	10.247	11.501	10.092
S. rufus	4	2	274-365	6.588	6.561	7.374
S. rufus	5	2	366-457	0.513	0.566	0.870
S. aurora	4	2	274-365	6.835	7.591	6.215
S. aurora	5	2	366-457	22.452	24.477	20.423
S. aurora	4	3	366-457	54.214	45.845	45.465
S. aurora	4	4	366-457	0.507	0.511	0.782
S. melanostomus	4	2	274-365	0.566	0.148	0.148
S. melanostomus	5	2	366-457	22.167	20.848	24.547
Average				1,398.584	1,369.394	1,314.689

observations. It was also noted that our present state of knowledge precludes more optimally designed stratified random schemes on the scale considered. It appears that the decision to space transects of the 1977 survey in a systematic fashion was correct. While the data do indicate that systematic sampling is more precise than stratified random, the differences are slight and

TABLE 5.—Variances of means of catch (per 1.8 km towed) from hypothetical populations of rockfish that were constructed from 1977 survey data. Calculations are made under random, stratified random, and systematic sampling schemes. Hypothetical populations are composed of two systematic samples with four or five members.

Population	Members	Area	Depth interval (m)	Variance		
				Random	Stratified random	Systematic
Sebastes alutus	4	4	183-273	1,569.231	1,576.140	3,193.380
S. alutus	4	4	366-457	15.517	5.162	3.195
S. flavidus	4	2	91-182	0.030	0.034	0.063
S. pinniger	4	1	91-182	2.807	3.261	6.439
S. pinniger	4	2	91-182	0.062	0.072	0.141
S. paucispinis	4	1	91-182	3,210.176	3,203.033	2,889.063
S. paucispinis	4	2	91-182	11.484	13.142	24.503
S. paucispinis	5	2	183-273	6.045	5.266	3.534
S. paucispinis	5	3	91-182	9.373	10.639	1.145
S. brevispinis	4	4	183-273	0.546	0.226	0.336
S. elongatus	4	1	91-182	1.217	1.436	2.441
S. elongatus	4	2	183-273	0.015	0.016	0.026
S. elongatus	5	3	91-182	0.766	0.656	0.656
S. elongatus	4	4	183-273	15.775	17.090	11.696
S. babcocki	4	2	183-273	0.994	1.102	0.130
S. babcocki	4	2	274-365	1.666	0.909	0.063
S. babcocki	4	3	366-457	0.263	0.197	0.002
S. babcocki	4	4	183-273	30.055	31.103	38.440
S. babcocki	4	4	366-457	1.940	0.551	1.000
S. crameri	4	2	274-365	10.827	12.414	2.403
S. crameri	5	2	366-457	0.879	0.372	0.372
S. crameri	4	4	183-273	475.931	378.362	426.423
S. crameri	4	4	366-457	0.077	0.107	0.035
S. zacentrus	4	4	183-273	3.770	0.485	0.281
S. diploproa	4	2	183-273	313.836	243.015	367.489
S. diploproa	4	2	274-365	953.833	869.422	1,065.206
S. diploproa	5	2	366-457	681.840	375.130	53.290
S. diploproa	4	3	366-457	53.007	25.279	0.191
S. diploproa	4	4	183-273	170.870	178.211	122.324
S. diploproa	4	4	366-457	0.609	0.803	0.090
S. entomelas	4	1	91-182	155.903	156.260	158.760
S. entomelas	4	2	91-182	0.337	0.402	0.856
S. entomelas	4	2	183-273	0.763	0.275	0.723
S. entomelas	5	3	91-182	0.094	0.106	0.000
S. entomelas	4	4	183-273	0.751	0.849	0.250
S. aleutianus	4	4	366-457	196.666	199.264	398.003
S. goodei	4	1	91-182	39.745	38.155	35.106
S. goodei	4	2	91-182	1,479.720	1,367.750	1,531.744
S. goodei	4	2	183-273	104.217	127.159	335.989
S. goodei	5	3	91-182	64.595	72.201	140.660
S. jordani	4	1	91-182	155.874	163.576	85.794
S. jordani	4	2	91-182	8,921.814	9,116.721	7,983.423
S. jordani	4	2	183-273	1.814	2.179	0.004
S. jordani	5	3	91-182	0.144	0.137	0.137
S. saxicola	4	1	91-182	3,677.792	335.847	431.081
S. saxicola	4	2	91-182	48.652	55.079	106.864
S. saxicola	4	2	183-273	2,794.359	3,362.293	3,068.052
S. saxicola	4	2	274-365	0.081	0.069	0.069
S. saxicola	5	2	366-457	0.026	0.007	0.000
S. saxicola	5	3	91-182	850.717	916.415	388.878
S. saxicola	4	3	366-457	1.035	1.101	0.640
S. saxicola	4	4	183-273	1.158	1.285	2.789
S. rufus	4	2	183-273	2.562	1.899	2.161
S. rufus	4	2	274-365	2.196	2.447	3.331
S. rufus	5	2	366-457	0.128	0.144	0.000
S. aurora	4	2	274-365	2.278	2.502	0.902
S. aurora	5	2	366-457	5.613	2.157	1.988
S. aurora	4	3	366-457	18.071	12.091	14.440
S. aurora	4	4	366-457	0.169	0.045	0.051
S. melanostomus	4	2	274-365	0.189	0.008	0.004
S. melanostomus	5	2	366-457	5.542	4.153	3.686
Average				427.483	375.349	375.586

probably should not outweigh other factors such as logistical constraints in the design of trawl surveys.

The sign test used to test the significance of differences among sample designs assumed that values for each species were independent. To examine this assumption we calculated correlation coefficients for each species pair in each combination of depth and area. Only samples containing at least one occurrence of each species of a pair were included. The average of the absolute value of the correlation coefficient is

0.324. This indicates that the assumption of independence is reasonable.

Even though our results indicate that systematic sampling is slightly more precise for the type of survey studied, the consequence of using a systematic design when another design may be more appropriate should be considered.

We first examine the effects of using a systematic design when in actuality the data are randomly distributed. Under these conditions the expected value of $S^2_{y_{st}}$ of Equation (5) is equal to the expected value of S^2_{sys} of Equation (6) and is related to the expected value of $S^2_{\bar{y}ran}$ of Equation (4) as follows:

$$E(S^2_{st}) = \frac{nk-1}{nk-n} \quad E(S^2_{ran}).$$

Thus, random sampling will produce the lowest variance and if total sampling effort (nk) is constant, the variance of systematic and stratified random sampling will decrease relative to random sampling as n decreases. All three design strategies will result in unbiased estimates of the mean.

If there is a linear trend in the data such as shown below

Transect	1	2	3	4	5	6	7	8
Value	1	1.5	2	2.5	3	3.5	4	4.5,

then as Cochran (1964:217) showed, stratified random sampling is the same or more precise than systematic sampling, which is the same or more precise than random. The discrepancies increase as n increases.

If there are cycles in the data with a periodicity equal to or a multiple of spacing of transects such as

Transect	1	2	3	4	5	6	7	8
Value	1	2	1	2	1	2	1	2,

then systematic sampling is less precise than stratified random sampling, which is less precise than random sampling. The discrepancies increase as n increases. In addition, a single systematic sample would result in a biased estimate of the mean.

Systematic sampling is equal to or more precise than stratified random sampling which is equal to or more precise than random sampling if a population in which a plot of correlations between pairs of transects against distance between transects is concave upward and greater than or equal to 0 (Cochran 1964). Since systematic sampling was the most precise in this study, bias due to periodicity in the data should not be a problem.

Often in practice, investigators use a systematic sampling scheme with only one sample and calculate the variance as if the scheme is random. If $V(\bar{y}_{sys})$ is $< V(\bar{y}_{ran})$, as it appears to be for rockfishes, the resulting confidence limits would be conservative. The choice between precision and estimation of $V(\bar{y}_{sys})$ would depend on the objectives of the survey and the difference between $V(\bar{y}_{ran})$ and $V(\bar{y}_{sys})$. If $V(\bar{y}_{sys})$ is $< V(\bar{y}_{ran})$ and total number of transects is constant, increasing the number of systematic samples (k) in order to estimate $V(\bar{y}_{sys})$ causes the sampling scheme to become more like a random scheme and results in a corresponding increase in $V(\bar{y}_{sys})$ relative to $V(\bar{y}_{ran})$ (compare average variances shown in Tables 4 and 5).

A review by Cochran (1964) of a small number of surveys of terrestrial populations also indicated that systematic sampling is more precise than stratified random. Although Cochran did not state so, it also appeared that systematic sampling would be more precise than random sampling.

Two studies were found in the literature on marine populations. Venrick (1978) found that on the average systematic samples of chlorophyll in the water column produced estimates of total chlorophyll that were closer to the true value than stratified random samples, but was not able to compare precision of estimates for a given water column because only one systematic sample was taken from each column. She expressed a preference for stratified random sampling, because there tended to be more temporal correlations of deviations of the estimated values from the true values for the systematic samples than for the stratified random samples. The deviations were usually $<5\%$ and the temporal correlations probably could have been eliminated if the starting points of the systematic samples were observed at random instead of being fixed at the surface as was done in her study. Fiedler (1978) examined the relative precision of random, systematic, and stratified systematic transect surveys of northern anchovy, *Engraulis mordax*, school groups. He found that random sampling was the least precise of the three schemes. He also found that stratified

systematic sampling was more precise than systematic sampling when school groups were distributed in a highly nonrandom way. Systematic sampling was more precise than stratified systematic sampling when sampling density was high. In other cases there were no significant differences between systematic and stratified systematic sampling.

Fiedler based allocations of sampling effort among strata on results of previous sampling. His results, in conjunction with those of Abramson (1968) and Venrick (1978), indicate the difficulty of determining optimum allocation of sampling effort among strata in the marine environment. The frustration of scientists who have attempted to do so is aptly stated by Venrick: "Study A demonstrated the dependence of the success of a sampling design upon the interaction of that design with the structure of the population being sampled; thus, it would seem that intelligent application of knowledge about the sampled population should improve the design. It was, therefore, disconcerting to find that RSS every 20 m, RSS-1, consistently performed as successfully as did RSS-3 which was designed by a presumably experienced worker (the author) with total knowledge about the population to be sampled."

We hope that improved knowledge on the distributions of populations will eventually result in more efficient allocation of effort among strata of systematic or random sampling schemes in the marine environment. However, we point out that fishermen still have their failures in attempting to restrict their sampling effort to times and areas of high fish catches in spite of years of experience, sophisticated fish finding equipment—presumably flexible sampling plans—and at times recent information from their colleagues.

EXAMINATION OF TRADE OFFS BETWEEN TOW LENGTH AND NUMBER OF TOWS

The distance trawled is an important factor to consider in the design of trawl surveys. Considerations include distance needed to obtain sufficient specimens for biological samples; time required to set and retrieve a trawl, to cover the distance, and to move between trawl locations; and the relationship among precision, tow length, and number of tows.

In this section we first use a negative binomial model with varying element size to estimate the relationship among precision and tow length and number of tows. We next use this relationship and time factors to illustrate the relationship between logistically feasible tow lengths and precision.

Animals in nature are rarely randomly distributed. They usually show some degree of aggregation or contagion. When these populations are sampled, they lead to distributions which are markedly skewed and have a large proportion of zero elements. The negative binomial distribution is often assumed for such populations because of practical performance (Laubscher 1961; Pielou 1969) and theoretical basis (Taylor 1953; Patil and Stiteler 1974). The distribution can be used to provide an estimate of the relationship between sample element size and precision.

The negative binomial distribution often is used to describe observed distributions in both general ecological research (Pielou 1969; Poole 1974) and fisheries research (Taylor 1953; Moyle and Lound 1960; Lambou 1963; Roessler 1965; Clark 1974). The distribution is characterized by two parameters, m the mean number of units per sampling element, and k, an "index of aggregation" (Waters 1959). The value of k varies inversely with the degree of aggregation of the population. The variance of a mean drawn from a population which follows a negative binomial distribution (V_{nb}) is a function of the mean (m) and k,

$$V_{nb} = m + m^2/k.$$

As the degree of aggregation increases, k approaches 0 and when the empty elements are ignored, this distribution approaches Fisher's logarithmic series. As the degree of aggregation decreases, k will approach infinity and the distribution converges to the Poisson.

The negative binomial can be derived from five or more different models, which may be mutually contradictory (Anscombe 1950; Bliss and Fisher 1953). A commonly used procedure to derive the distribution is to assume that it arises from a cluster of objects in space where the clusters follow a Poisson distribution and the number of animals in a cluster are distributed according to Fisher's logarithmic series. Taylor (1953) derived a form of the negative binomial as a probability model specifically to describe the relative abundance of fish species in trawl catches.

The data used for this analysis come from the pilot survey made in Queen Charlotte Sound. Since the negative binomial distribution is a

discrete function, catches are measured in numbers of fish instead of weight as in the preceding section.

Fitting data from a systematically designed survey to the negative binomial distribution is a common practice (Moyle and Lound 1960; Taft 1960; Roessler 1965; Clark 1974). Hairston et al. (1971) made one of the few studies of sampling design for measuring spatial pattern. They found that estimates based on a grid (systematic) pattern were superior to those made from sampling at random. The grid pattern correctly reflected the spatial patterns of 17 of 22 species, while random sampling with the same number of samples correctly reflected only 12 of 22 species.

The standard negative binomial model requires a constant element size. This leads to two problems. The first is that comparisons can only be made at one sampling element size. The second problem is the negative binomial model cannot be fit to data with variation in sample element size.

To specifically deal with these problems, Bissell (1970, 1972) derived a negative binomial model that can be used when sample element size is variable and/or to predict the distribution of events for element sizes which differ from those on which the observations were based. The probability of observing x_i events on the i element which has a size of w_i is

$$P(x_i/w_i) = \{k/(mw_i + k)\}^k \{mw_i/(mw_i + k)\}^{x_i} \prod_{j}^{x_i} \{(k + j - 1)/j\} \quad (7)$$

where m = mean value of x_i for element size of unit size

k = parameter representing the degree of aggregation (Note that k in this section has a different meaning than in the section on sampling schemes)

w_i = element size (distance towed).

Iterative maximum likelihood solutions (Bissell 1972) gave estimates of values of m, k, and their standard errors relative to the average distance towed. The values were converted to densities (d) with units of numbers per kilometer. Estimates of d, k, and chi-square goodness of fit tests are given in Table 6. These tests were made by calculating the probability of a given number of fish occurring in a trawl of a given length from the probability density function given by Bissell (1972). This probability was cumulated over all trawls and then compared with the observed value using a chi-square test. Values of k from trawls in all depths ranged from 0.2 to 0.6 for the most abundant species. The low values of k indicate that the more abundant species are highly aggregated. The estimates for k are close to the value of k (0.27) that we estimated for *S. marinus*, an abundant species of rockfish, from Georges Bank from data in the paper by Taylor (1953).

TABLE 6.—Estimates of mean densities ($\bar{d}$) (in numbers per kilometer), k, standard errors, with chi-square goodness of fit tests for trawl catches made in all depths in the Queen Charlotte survey.

Species	Mean density	SE($\bar{d}$)	k	SE(k)	Chi-square probability
Sebastes alutus	75.368	18.466	0.334	0.055	N.S.
S. flavidus	0.648	0.028	2.608	0.803	$P < 0.01$
S. pinniger	1.564	0.287	0.398	0.071	N.S.
S. paucispinis	0.508	0.072	2.546	0.814	N.S.
S. brevispinis	2.446	0.426	0.528	0.098	N.S.
S. elongatus	0.519	0.070	3.393	1.253	$P < 0.01$
S. proriger	30.402	9.612	0.198	0.031	$P < 0.05$
S. babcocki	1.723	0.273	0.665	0.131	$P < 0.01$
S. crameri	0.509	0.070	3.233	1.008	$P < 0.01$
S. zacentrus	4.973	1.428	0.274	0.044	$P < 0.01$
S. diploproa	0.623	0.102	1.157	0.292	$P < 0.01$
S. entomelas	0.119	0.028	6.289	1.004	N.S.
S. reedi	1.867	0.412	0.390	0.069	$P < 0.01$
S. aleutianus	0.205	0.037	6.550	1.215	N.S.
S. helvomaculatus	0.301	0.048	4.424	1.078	$P < 0.01$

Estimates of mean densities, k, and goodness of fit tests by depth strata are presented in Table 7.

The chi-square tests show that the data combined over all depths are not well represented by the negative binomial model. However, when the data are divided up by depth strata, the agreement is quite good. When the data from low density and high density depth strata are combined, the resulting frequency distribution has too many zero elements and too many high abundance elements. This results in the high chi-square values from trawls at all depths. In comparing the results in Tables 6 and 7, it is obvious that depth stratification is important. The differences between densities of species among depth strata were tested at the 10% level of significance. Of 43 possible comparisons, 27 (or 63%) were significantly different. This can be tested against what would have occurred randomly as a binomial proportion (Hollander and Wolfe 1973). The proportion is significantly different than random (z = 6.77,

TABLE 7.—Estimates of mean densities (d) (in numbers per kilometer), k, standard errors, with chi-square goodness of fit tests for trawl catches by depth strata in the Queen Charlotte survey.

Species	Depth strata (m)	Mean density	SE(d)	k	SE(k)	Chi-square probability
Sebastes alutus	91-145	7.119	3.098	0.290	0.080	N.S.
S. alutus	146-181	90.816	37.533	0.419	0.132	N.S.
S. alutus	>181	131.914	36.838	0.693	0.197	N.S.
S. flavidus	91-145	1.160	0.253	1.660	0.817	N.S.
S. flavidus	146-181	0.724	0.200	2.037	1.030	N.S.
S. flavidus	>181	0.051	0.003	4.900	1.231	(1)
S. pinniger	91-145	5.200	2.084	0.322	0.090	N.S.
S. pinniger	146-181	0.465	0.136	2.155	1.063	(1)
S. pinniger	>181	0.018	0.017	(2)	—	—
S. paucispinis	91-145	1.051	0.308	0.870	0.323	N.S.
S. paucispinis	146-181	0.262	0.088	2.494	0.944	N.S.
S. paucispinis	>181	0.196	0.064	3.580	1.077	N.S.
S. brevispinis	91-145	4.401	1.435	0.531	0.160	N.S.
S. brevispinis	146-181	3.027	0.993	0.652	0.232	N.S.
S. brevispinis	>181	1.145	0.354	0.679	0.231	$P \leq 0.05$
S. elongatus	91-145	0.426	0.106	2.623	1.130	N.S.
S. elongatus	146-181	1.023	0.326	0.857	0.353	N.S.
S. elongatus	>181	0.193	0.062	4.535	1.334	N.S.
S. proriger	91-145	81.620	64.163	0.090	0.022	N.S.
S. proriger	146-181	4.701	1.901	0.440	0.146	N.S.
S. proriger	>181	0.053	0.031	5.968	1.537	(1)
S. babcocki	91-145	0.220	0.068	3.108	0.956	N.S.
S. babcocki	146-181	1.426	0.446	1.274	0.627	N.S.
S. babcocki	>181	4.526	1.395	0.600	0.170	N.S.
S. crameri	91-145	0.017	0.016	(2)	—	—
S. crameri	146-181	0.916	0.280	1.042	0.476	$P \leq 0.01$
S. crameri	>181	0.673	0.146	2.549	1.168	N.S.
S. zacentrus	91-145	0.118	0.047	4.040	1.098	N.S.
S. zacentrus	146-181	1.065	0.363	0.622	0.239	N.S.
S. zacentrus	>181	12.991	6.382	0.229	0.061	N.S.
S. diploproa	91-145	0.000				
S. diploproa	146-181	0.000				
S. diploproa	>181	1.563	0.504	0.496	0.154	$P < 0.01$
S. entomelas	91-145	0.034	0.024	4.442	1.087	(1)
S. entomelas	146-181	0.202	0.073	3.306	1.105	$P \leq 0.05$
S. entomelas	>181	0.142	0.053	4.451	1.241	N.S.
S. reedi	91-145	0.000				
S. reedi	146-181	0.066	0.039	4.124	1.177	(1)
S. reedi	>181	5.445	2.332	0.302	0.084	$P < 0.01$
S. aleutianus	91-145	0.000				
S. aleutianus	146-181	0.087	0.040	(2)	—	—
S. aleutianus	>181	0.517	0.125	2.379	1.035	N.S.
S. helvomaculatus	91-145	0.000				
S. helvomaculatus	146-181	0.022	0.022	3.277	0.908	N.S
S. helvomaculatus	>181	0.844	0.227	1.098	0.457	$P \leq 0.01$

[1] Insufficient nonzero elements to perform chi-square test.
[2] Randomly distributed, $k \to \infty$.

$P < 0.01$). Although the rockfish species tended to be aggregated, the group covers a wide range of spatial patterns.

In sampling from a negative binomial distribution, the precision of a density estimate for any given population depends both on the properties of the population, its density (d) and degree of aggregation (k), and on the characteristics of sampling, sample size (n) and the sample element size (S) (tow length). By modifying the sample characteristics, one can modify the precision of estimates.

Taylor (1953) showed in his Appendix E that reducing sample element size (length of the trawl) was the optimal sampling strategy under the condition that the total sampling area remained constant. That is, if A = area of strata (which is constant over all strata, i.e., $A_1 = A_2 = A_3 \ldots$), a = area of the sampling element, and n = the number of samples taken in each stratum, then the value $(a/A)n$ is fixed. Therefore, by reducing the length of tow, there must be a corresponding increase in the number of tows. However, in the body of his paper, Taylor implies that it would be advantageous to reduce sample element size even with a constant number of samples. His argument is based on the relationship between the mean and variance for a negative binomial population (V_{nb_1})

$$V_{nb_1} = m + m^2/k.$$

The argument is that as m is reduced by some factor $1/b$, then V_{nb_2} would only be

$$V_{nb_2} = m/b + (m/b)^2/k.$$

While this argument is correct, it does not mean that the estimate of total numbers of fish over the entire strata is more precise with decreasing sample element size. The effect of reducing sample element size on the variance of the estimate of the total number of fish in a stratum under the condition of a fixed sample size is considered below. Using the definitions of A, a, n from above, then N = total possible number of samples in a stratum where the sample element size equals a (i.e., $N = A/a$). The variance of the total number of fish in a stratum from n samples of the standard element size (V_{t_1}) is

$$V_{t_1} = \frac{N_1^2}{n} V_{nb_1} \quad \text{or} \quad V_{t_1} = \frac{A^2}{a^2 n}\left[m + \frac{m^2}{k}\right]$$

(Cochran 1964). The variance (V_{t_2}) of the total number of fish in a stratum for the sample element size reduced by $1/b$ is

$$V_{t_2} = \frac{N_2^2}{n} V_{nb_2} = \frac{\left[\frac{A}{\left(\frac{a}{b}\right)}\right]^2}{n}\left[\frac{m}{b} + \frac{m^2}{b^2 k}\right]$$

$$= \frac{A^2 b^2}{a^2 n}\left[\frac{m}{b} + \frac{m^2}{b^2 k}\right] = \frac{A^2}{a^2 n}\left[bm + \frac{m^2}{k}\right].$$

The difference in variance between the different sample element sizes is

$$V_d = V_{t_2} - V_{t_1}$$

$$= \frac{A^2}{a^2 n}\left[bm + \frac{m^2}{k}\right] - \frac{A^2}{a^2 n}\left[m + \frac{m^2}{k}\right]$$

$$= \frac{A^2}{a^2 n}\left[m(b-1)\right]. \tag{8}$$

Although there is actually an increase in overall variance by reducing sample element size with a constant sample size, it will be relatively small compared with the overall variance when m is large in value and/or k small:

$$\text{relative increase} = \frac{\frac{A^2}{a^2 n}\left[m(b-1)\right]}{\frac{A^2}{a^2 n}\left[m\left(1 + \frac{m}{k}\right)\right]}$$

$$= \frac{b-1}{1 + \frac{m}{k}}.$$

The purpose of many surveys is to produce total biomass estimates. These total biomass estimates are made by expanding a density estimate (usually in the form of a catch per unit effort measure) (Gunderson and Sample 1980) by the total area (Cochran 1964). Since measurement of the area involved can be made with relatively little error compared with the density estimate, we ignore error in area measurements in the following discussion. The precision of an estimate will vary inversely to its standard error. An index of precision ($P_{\bar{d}}$) is:

$$P_{\bar{d}} = \bar{d}/\mathrm{SE}_{\bar{d}}. \tag{9}$$

This index is the inverse of the coefficient of variation and is used here because it varies directly rather than inversely with precision. The density of a population is equal to the mean of the negative binomial distribution divided by the sample element size (S):

$$\bar{d} = m/S \tag{10}$$

where m = the mean of a number of tows of sample element size (S),
S = a constant sample element size with no variance.

The variance of m is

$$V_m = (m + m^2/k)/n. \tag{11}$$

Therefore the variance of the density estimate is

$$V_{\bar{d}} = (m + m^2/k)/nS^2 \tag{12}$$

and from Equation (10)

$$V_{\bar{d}} = (\bar{d}S + (\bar{d}S)^2/k)/nS^2 \quad (13)$$

or

$$V_{\bar{d}} = \frac{\bar{d}}{nS} + \frac{\bar{d}^2}{nK} . \quad (14)$$

The standard error of the density is

$$SE_{\bar{d}} = (V_{\bar{d}})^{1/2} \quad (15)$$

$$= \left(\frac{\bar{d}}{nS} + \frac{\bar{d}^2}{nK}\right)^{1/2} \quad (16)$$

and the index of precision is

$$P_{\bar{d}} = (\bar{d})/(\bar{d}/nS + \bar{d}^2/nk)^{1/2}$$

$$= (1/\bar{d}nS + 1/nk)^{-1/2}. \quad (17)$$

From Equation (17), the precision of a density estimate will decrease as the degree of aggregation increases (i.e., $k \rightarrow 0$). For the case when $k >> \bar{d}$, then the index approaches $(\bar{d}nS)^{1/2}$ and a unit increase in sample size and sample element size are of equal importance. In the case of $\bar{d}$ approximately equal to k then sample element size has almost no effect on precision. When $\bar{d} >> k$, which is often the case for species that support a commercial fishery, the index simplifies to

$$P_{\bar{d}} \rightarrow (nk)^{1/2}. \quad (18)$$

In these cases, only sample size will affect precision.

More specific evaluation of sampling negative binomial populations can be made by considering the estimates of k for three rockfish species and Equation (17). Since the limiting factor in these surveys is usually ship time and not cost in a direct sense, the evaluation is in terms of the most efficient use of a ship day. The first two species were the two target species in the Queen Charlotte Sound survey: *S. alutus*, a high density, highly aggregated species, and *S. flavidus*, a low density, highly aggregated species. The third species was *S. aleutianus*, a low density more randomly distributed species in Queen Charlotte Sound.

The sampling plan in Queen Charlotte Sound was to perform trawls of 0.5 h on the bottom which covered an average of 2.80 km. The average number of trawls per working day was 4.3. The average working day was 13 h long. Assuming 0.5 h on the bottom per trawl and 4.3 trawls/d, then the average nontrawling time per haul is 2.05 h. The minimum nontrawling time per haul was 1.07 h. The current sampling plan calls for an average of about 5 trawls/d. Using the above times, four possible alternative strategies are: 1) 3 trawls/d with gear at depth for 2.1 h, 2) 4 trawls/d with gear at depth for 1.2 h, 3) 5 trawls/d with gear at depth for 0.5 h, or 4) 6 trawls/d with gear at depth for 0.3 h.

Using the four strategies, values for precision of estimate of density were calculated for *S. alutus*, *S. flavidus*, and *S. aleutianus* and are shown in Figures 1, 2, and 3. The results of this analysis follow directly from the result of the general analysis. When the density to k ratio increases above a critical level, precision is for all practical purposes unaffected by changes in density. For the more randomly distributed species (*S. aleutianus*) the critical ratio occurs at higher density. For more aggregated species (*S. alutus*, *S. flavidus*) sample size (n) is not as effective in increasing $P_{\bar{d}}$ in an absolute sense as in the less aggregated species. Also, since sample size and sample element size are inversely related and precision increases with increased sample size except at very low density, sample element size has little effect on precision for these species except at very low density. Even for the less aggregated species, sample element size has little effect on precision except at low densities.

For a fixed amount of sampling effort, the precision of an estimate from a negative binomial population is a result of the interaction of population factors, density ($\bar{d}$) and degree of aggregation (k); and sampling factors, sample size (n) and sample element size (S). Analysis of the results of the Queen Charlotte Sound survey shows that rockfish species have a wide range of possible combinations of population factors. The analysis of sampling strategies showed that the same sampling plan could have been used for all three species with no significant loss in precision. This is due to the highly aggregated nature of rockfish species. However, for other less aggregated species, such as flatfishes, there would have been a greater difference among sampling schemes. This emphasizes the importance of picking target species on

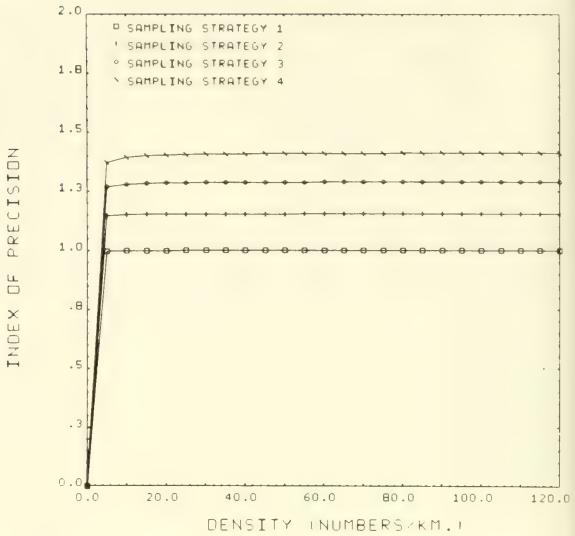


FIGURE 1.—Comparison of precision-density curves of four different sampling strategies for *Sebastes alutus*: 1) Three trawls/d with gear at depth for 2.1 h, 2) four trawls/d with gear at depth for 1.2 h, 3) five trawls/d with gear at depth for 0.5 h, and 4) six trawls/d with gear at depth for 0.3 h.

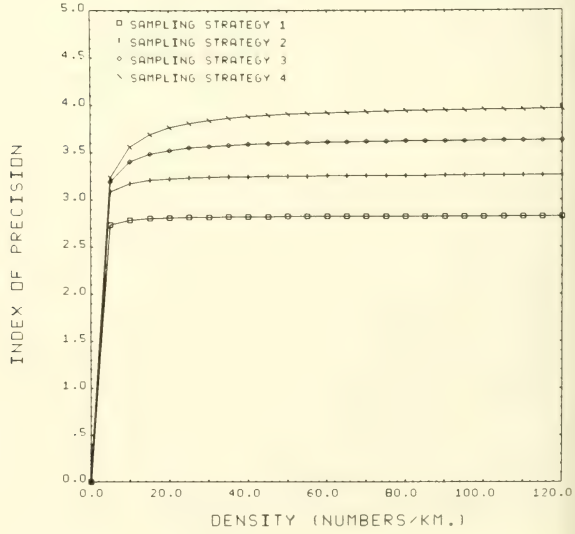


FIGURE 2.—Comparison of precision-density curves of four different sampling strategies for *Sebastes flavidus*: 1) Three trawls/d with gear at depth for 2.1 h, 2) four trawls/d with gear at depth for 1.2 h, 3) five trawls/d with gear at depth for 0.5 h, and 4) six trawls/d with gear at depth for 0.3 h.

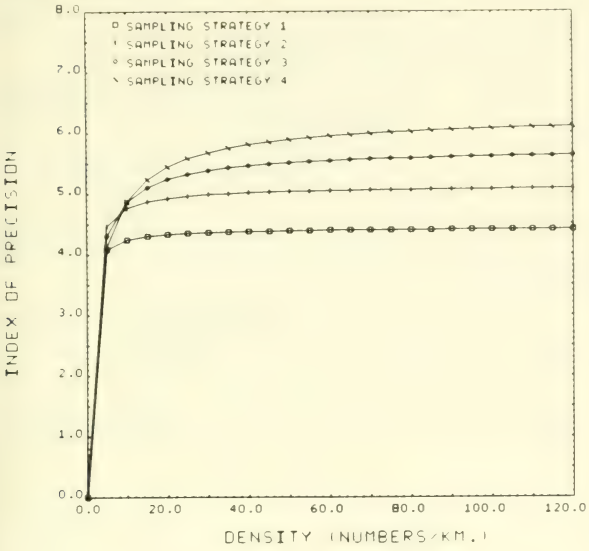


FIGURE 3.—Comparison of precision-density curves of four different sampling strategies for *Sebastes aleutianus*: 1) Three trawls/d with gear at depth for 2.1 h, 2) four trawls/d with gear at depth for 1.2 h, 3) five trawls/d with gear at depth for 0.5 h, and 4) six trawls/d with gear at depth for 0.3 h.

which to focus sampling strategies. For rockfish, these are likely to be high density, highly aggregated species. Generally, in sampling strategies for these species, the effects of sample element size would be unimportant. Increases in sample size would be much more important in terms of increased precision; however, increases in sample size would have to be fairly large to make a significant difference.

ACKNOWLEDGMENTS

We owe considerable thanks to Candis Cooperrider of the Tiburon Laboratory for writing computer programs for the study. Reviews by N. Abramson (Southwest Fisheries Center Tiburon Laboratory), T. Foin (University of California at Davis), D. Gunderson (University of Washington), D. Kimura (Washington Department of Fisheries, Seattle), J. Zweifel (Southwest Fisheries Center La Jolla Laboratory), and two anonymous referees resulted in a number of useful suggestions.

LITERATURE CITED

ABRAMSON, N. J.
1968. A probability sea survey plan for estimating relative abundance of ocean shrimp. Calif. Fish Game 54: 257-269.

ANSCOMBE, F. J.
1950. Sampling theory of the negative binomial and logarithmic series distributions. Biometrika 37:358-382.

BISSELL, A. F.
1970. Analysis of data based on incident counts. The Statistician 19:215-247.
1972. A negative binomial model with varying element sizes. Biometrika 59:435-441.

BLISS, C. I., AND R. A. FISHER.
1953. Fitting the negative binomial distribution to biological data and note on the efficient fitting of the negative binomial. Biometrics 9:176-200.

CLARK, S. H.
1974. A study of variation in trawl data collected in Everglades National Park, Florida. Trans. Am. Fish. Soc. 103:777-785.

COCHRAN, W. G.
1964. Sampling techniques. 2d ed. Wiley, N.Y., 413 p.

FIEDLER, P. C.
1978. The precision of simulated transect surveys of northern anchovy, *Engraulis mordax*, school groups. Fish. Bull., U.S. 76:679-685.

GUNDERSON, D. R., AND T. M. SAMPLE.
1980. Distribution and abundance of rockfish off Washington, Oregon and California during 1977. Mar. Fish. Rev. 42(3-4):2-16.

HAIRSTON, N. G., R. W. HILL, AND U. RITTE.
1971. The interpretation of aggregation patterns. *In* G. P. Patil, E. C. Pielou, and W. E. Waters (editors), Statistical ecology. Vol. 1. Spatial patterns and statistical distributions, p. 337-353. Pa. State Univ. Press, Univ. Park, Pa.

HANSEN, M. H., W. N. HURWITZ, AND W. G. MADOW.
1953. Sample survey methods and theory. Vol. 1. Methods and applications. Wiley, N.Y., 638 p.

HOLLANDER, M., AND D. A. WOLFE.
1973. Nonparametric statistical methods. Wiley, N.Y., 503 p.

LAMBOU, V. W.
1963. Application of distribution pattern of fishes in Lake Bistineau to design of sampling programs. Prog. Fish-Cult. 25:79-87.

LAUBSCHER, N. F.
1961. On stabilizing the binomial and negative binomial variances. J. Am. Stat. Assoc. 56:143-150.

MOYLE, J. B., AND R. LOUND.
1960. Confidence limits associated with means and medians of series of net catches. Trans. Am. Fish. Soc. 89:53-58.

PATIL, G. P., AND W. M. STITELER.
1974. Concepts of aggregation and their quantification: a critical review with some results and applications. Res. Popul. Ecol. 15:238-254.

PIELOU, E. C.
1969. An introduction to mathematical ecology. Wiley-Interscience, N.Y., 286 p.

POOLE, R. W.
1974. An introduction to quantitative ecology. McGraw-Hill, San Francisco, 532 p.

ROESSLER, M.
1965. An analysis of the variability of fish populations taken by otter trawl in Biscayne Bay, Florida. Trans. Am. Fish. Soc. 94:311-318.

SUKHATME, P. V., AND B. V. SUKHATME.
1970. Sampling theory of surveys with applications. 2d ed. Iowa State Univ. Press, Ames, 452 p.

TAFT, B. A.
1960. A statistical study of the estimation of abundance of sardine (*Sardinops caerulea*) eggs. Limnol. Oceanogr. 5:245-264.

TAYLOR, C. C.
1953. Nature of variability in trawl catches. U.S. Fish Wildl. Serv., Fish. Bull. 54:145-166.

VENRICK, E. L.
1978. Systematic sampling in a planktonic ecosystem. Fish. Bull., U.S. 76:617-627.

WATERS, W. E.
1959. A quantitative measure of aggregation in insects. J. Econ. Entomol. 52:1180-1184.

EFFECTS OF COPPER ON EARLY LIFE HISTORY STAGES OF NORTHERN ANCHOVY, *ENGRAULIS MORDAX*

D. W. RICE, JR.,[1] F. L. HARRISON,[1] AND A. JEARLD, JR.[2]

ABSTRACT

The sensitivity to copper of embryonic and larval stages of the Northern anchovy, *Engraulis mordax*, was determined using a flow-through bioassay system. Northern anchovy embryos were exposed continuously from 8 to 10 hours after fertilization until hatching, and the larvae were exposed within 12 hours after hatching until yolk-sac absorption. During the testing both total copper concentrations and the percent copper in labile forms were determined. From the cumulative mortality versus measured copper exposure data, a series of median lethal concentrations (LC_{50}) were determined. These LC_{50} values were used to construct comparative toxicity curves.

The northern anchovy life stage most sensitive to copper was the embryonic stage. For northern anchovy embryos the 12-hour LC_{50} was 200 μg Cu/l, and the estimated incipient lethal concentrations (ILC_{50}) was 190 μg Cu/l; a sensitive period of embryonic development was noted prior to closure of the blastopore. The 12 hours, 24 hours, and ILC_{50} for northern anchovy larvae were 460, 400, and 370 μg Cu/l.

Copper is one of the wastes commonly discharged into coastal waters that has been shown to be toxic to marine fishes (Becker and Thatcher 1973; Lewis and Whitfield[3]). Increased copper concentrations in coastal marine waters have resulted from the release of municipal wastewater (Schafer[4]), power plant effluents (Young et al.[5]), and marine antifouling paints (Young and Alexander[6]). In polluted waters, concentrations have been recorded as high as 16,800 μg Cu/l in municipal waste effluents (Schafer footnote 4) and 1,800 μg Cu/l during start up of a power plant (Martin et al. 1977).

One important factor in the toxic effect of copper on marine fishes is the life history stage when the exposure occurs. Few studies have examined the comparative sensitivities of the major life stages of marine fishes: embryo, larva, and adult. The spot, *Leiostomus xanthurus*, was found to be more sensitive to copper in the embryonic stage than in the larval stage (Engel et al. 1976). The incipient lethal concentration (ILC_{50}—that concentration that kills 50% of a population during an exposure sufficiently long that acute lethal action has ceased [Sprague 1969]) for Pacific herring, *Clupea harengus pallasi*, embryos exposed to copper was found to be approximately 30 times lower than the ILC_{50} for Pacific herring larvae (Rice and Harrison 1978) and 7 times lower than the ILC_{50} for Pacific herring adults (Harrison and Rice[7]). Natural mortalities that occur during the early life stages have been suggested to be a major factor in reducing the size of a given year class of fish (May 1974; Cushing 1975; Vaughan and Saila 1976). Pollutants that have an impact on the survival of fish embryos or larvae might further reduce the size of a given year class of fish.

In addition to the life stage, the chemical form of copper to which fishes are exposed may play an important role in the toxic response (Lee 1973; Neff and Anderson 1977; Chapman and McCrady[8]). Copper in seawater can exist in many

[1]Environmental Sciences Division, Lawrence Livermore Laboratory, University of California, Livermore, CA 94550.
[2]Northeast Fisheries Center Woods Hole Laboratory, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543.

[3]Lewis, A. G., and P. H. Whitfield. 1974. The biological importance of copper in the sea, a literature review. International Copper Research Association, Proj. No. 223, Final Rep., 132 p.

[4]Schafer, H. A. 1977. Characteristics of municipal wastewater discharges, 1976. Coastal Water Research Project, Annual Report, 1977, 253 p. Southern California Coastal Water Research Project, 1500 East Imperial Highway, El Segundo, CA 90245.

[5]Young, D. R., Tsu-Kai Jan, and M. D. Moore. 1977. Metals in power plant cooling water discharges. Coastal Water Research Project, Annual Report, 1977, 253 p. Southern California Coastal Water Research Project, 1500 East Imperial Highway, El Segundo, CA 90245.

[6]Young, D. R., and G. V. Alexander. 1977. Metals in mussels from harbors and outfall areas. Coastal Water Research Project, Annual Report, 1977, 253 p. Southern California Coastal Water Research Project, 1500 East Imperial Highway, El Segundo, CA 90245.

[7]Harrison, F. L., and D. W. Rice, Jr. In prep. Toxic response and copper body burdens of adult Pacific herring, *Clupea harengus pallasi*, and northern anchovy, *Engraulis mordax*, exposed to increased copper concentrations.

[8]Chapman, G. A., and J. K. McCrady. 1977. Copper toxicity: a question of form. Recent advances in fish toxicology, a sym-

Manuscript accepted February 1980.
FISHERY BULLETIN: VOL. 78, NO. 3, 1980.

forms. We will use the terminology proposed by Batley and Florence (1976). According to these authors, labile copper, as defined by experimental conditions, includes ionic, as well as some dissociable, complexed forms; bound copper is that fraction of the total copper which is not labile and includes soluble copper-organic complexes, copper bound to high molecular weight organic materials, and copper occluded in or adsorbed onto highly dispersed colloids. Although current copper emission standards are defined in terms of the total copper concentration in the water (Anonymous 1972, 1976) complexation of copper has been shown to reduce its toxicity to marine organisms (Lewis et al. 1972, 1973; Davey et al. 1973; Sunda and Guillard 1976; Harrison et al.[9]). Ionic copper has been suggested as the form most toxic to freshwater fishes (Pagenkopf et al. 1974). During our testing of the early life stages of the northern anchovy, we determined both total copper concentrations and the percent copper in the labile forms.

Northern anchovy, *Engraulis mordax*, is a pelagic, filter-feeding fish that spawns in upwelling waters along the Pacific coast of the United States and Mexico (Ahlstrom 1960). During recent years, the northern anchovy catch has been the third largest commercial catch on the Pacific coast (McAllister 1976; Pinkas 1977). Having conducted earlier tests on the sensitivity to copper of Pacific herring during its early life stages (Rice and Harrison 1978), we set two objectives for the present study: to conduct similar tests on the northern anchovy and to compare the sensitivities of these two species of fish during their early life histories. We continuously exposed northern anchovy embryos and larvae to copper over a range of concentrations and then constructed comparative toxicity curves.

METHODS

Northern anchovy embryos were collected in San Francisco Bay, Calif., between the Tiburon Peninsula and Angel Island. Collections and tests were carried out over a period of 2 yr. Collections were made with a 0.5 m, 505 μm mesh, nylon plankton net, towed for 2 min just below the surface of the water. Collections from each tow were placed into a plastic bag half full of seawater; the bag was inflated with air and then held in an insulated ice chest containing seawater from the collection site. Water temperature at the collection site was between 17° and 18.5° C; upon arrival at Lawrence Livermore Laboratory the temperature of the water in the ice chest was always <19° C.

The water for the bioassay system was obtained from the University of California Marine Station at Bodega Bay, Calif. This water is pumped from the ocean off the open coast in an area that receives little anthropogenic input. The water contains low levels of trace metals, dissolved organics, and particulate material. The collected seawater was stored in a 40,000 l underground tank and passed through a filter with 1.0 μm openings prior to experimental use.

Two embryo tests were conducted during 1976 (test I: 7 July 1976; test II: 23 July 1976) and one embryo test during 1977 (test III: 27 June 1977). All larval tests were conducted during 1977 (test I: 6 June 1977; test II: 13 June 1977).

All transfers of embryos or larvae were carried out with a large-bore, polished glass pipette. During embryo tests, healthy embryos estimated to be 8-10 h old (stages IV-V, Ahlstrom 1943) were placed either directly into exposure chambers containing seawater with known concentrations of copper or allowed to hatch in control seawater. Larvae used during larvae tests hatched within the 12-h period preceding the test; hatched larvae were placed directly into exposure chambers containing seawater with known concentrations of copper. Approximately 50 embryos or 30 larvae were used in each exposure chamber.

Anchovy embryos and larvae were exposed to copper in 500 ml clear glass, flow-through, exposure chambers (Figure 1) which, in turn, were immersed in a water bath (mean temperature: 16.8°±1.0° C). Seawater containing a known concentration of copper, as copper chloride, was pumped into each chamber from a 19 l plastic jug at a rate of 5 ml/min. About 5 h were required to replace 95% of the water in the exposure chamber; the mixture of seawater and copper in the 19 l plastic jugs was prepared daily.

The height of the water in the exposure chambers was maintained by a constant-level, outflow siphon. The mouth of the siphon, located at the base of the exposure chamber, was covered with nylon netting (265 μm pore size) to prevent the loss

posium. U.S. Environ. Prot. Agency Ecol. Res. Ser., EPA 600/3-77-085, July 1977. 204 p.

[9]Harrison, F. L., J. P. Knezovich, and J. S. Tucker. 1979. Sensitivity of *Crassostrea gigas* embryos to different chemical forms of copper. Univ. Calif., Lawrence Livermore Lab., Livermore. UCRL 52725; NUREG/CR-1088.

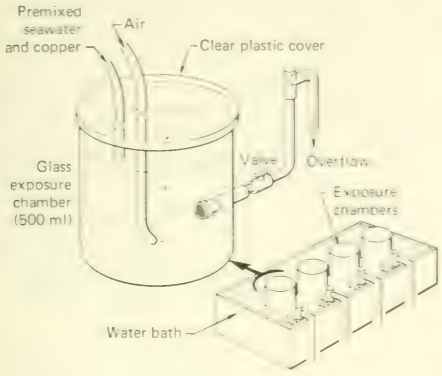


FIGURE 1.—Diagram of the exposure chamber and flow-through bioassay system used to expose northern anchovy embryos and larvae to copper.

of organisms from the chamber. The bottom outlet from each exposure chamber was fitted with a valve that could be closed to allow removal of the chamber from the water bath. This was important because during each observation the exposure chambers were removed and illuminated from the side. In this manner both live and dead organisms could be examined. Observations were made every 2-4 h during the copper exposures. During embryo exposures, a gentle stream of bubbles was delivered to the bottom of the exposure chamber; during larval exposures, no aeration was used. Overhead illumination was provided by the fluorescent lighting in the laboratory and followed the regular ambient photoperiod. The number of embryos or larvae exposed during each test is given in Tables 1 and 2.

Exposures continued until 1) all animals died, or 2) in the case of the embryos, until hatching was complete, or 3) in the case of the larvae, until the

TABLE 1.—Samples mortality data used to calculate LC_{50} values for northern anchovy embryos exposed to different copper concentrations. Chi-square tests used the null hypothesis that the relationship between dose and response followed the logit model.

Exposure time (h)	Control	Measured exposure concentration (μg Cu l ± SD) 92 ±8	116 ±14	171 ±31	177 ±30	190 ±12	197 ±41	242 ±46	272 ±22	285 ±19	531 ±66	564 ±39	589 ±28	LC_{50} (μg Cu l)	Chi-square value[3]	df
		Proportion dead[4]														
2	0.00	0.04	0.02	0.00	0.02	0.03	0.16	0.21	0.03	0.27	0.77	0.93	0.85	409±22	29.14**	11
4	.00	.04	.03	.01	.14	.24	.32	.44	.29	.61	.96	.93	.94	292±16	38.82***	11
6	.00	.14	.03	.08	.14	.47	.44	.63	.51	.86	.98	.96	.98	235±10	40.67***	11
8	.00	.21	.09	.12	.25	.59	.49	.72	.64	.88	.98	1.00	1.00	213± 8	29.24**	11
12	.00	.25	.09	.15	.27	.62	.62	.76	.75	.95	1.00			199± 8	40.06***	9
18	.00	.27	.09	.17	.31	.67	.65	.80	.78	.98	1.00			193± 7	40.65***	9
25	.00	.27	.09	.17	.38	.67	.69	.84	.85	.98	1.00			186± 6	40.49***	9
32	.00	.27	.09	.17	.39	.67	.70	.84	.88	.98	1.00			185± 9	41.88***	9
No. organisms exposed	260	28	90	94	124	34	161	113	66	96	126	29	104			

[1] Labile copper = 1.3 (SD = 0.1) μg Cu l.
[2] = 95% confidence limit.
[3] **P ≤ 0.01; ***P ≤ 0.001.
[4] Corrected for control mortality.

TABLE 2.—Samples mortality data used to calculate LC_{50} values for northern anchovy larvae exposed to different copper concentrations. Chi-square tests used the null hypothesis that the relationship between dose and response followed the logit model.

Exposure time (h)	Control	Measured exposure concentration (μg Cu l ± SD) 277±6	289±29	427±7	531±42	724	LC_{50} (μg Cu l)	Chi-square value[3]	df
		Proportion dead[4]							
4	0.00	0.14	0.02	0.42	0.49	0.76	523±58	7.90	4
8	.00	.15	.18	.49	.53	.84	485±54	4.02	4
12	.00	.16	.16	.50	.65	.87	457±46	2.61	4
20	.00	.07	.30	.59	.79	1.00	412±34	7.35	4
26	.00	.06	.30	.71	.85	1.00	391±31	7.61	4
32	.00	.08	.41	.75	.87	1.00	375±31	11.15	4
40	.00	.11	.41	.73	.87	1.00	374±32	8.86	4
46	.00	.01	.51	.79	.87	1.00	372±30	27.28***	4
No. organisms exposed	74	71	33	61	60	26			

[1] Labile copper = 1.3 (SD = 0.1) μg Cu l.
[2] Simple measurement.
[3] = 95% confidence limit.
[4] *P ≤ 0.05; ***P ≤ 0.001.
[5] Corrected for control mortality.

yolk sac was absorbed. The criterion for embryo mortality was the appearance of opacity of the embryo, and the criterion for larval mortality was failure to respond to a prod with a polished glass rod. Cumulative mortality with time, percentage hatching, and the stage of development at mortality were taken to be indices of the toxic effect of copper.

Total copper concentrations were measured every other day during all tests. Labile copper concentrations were measured every other day during embryonic test III and larval tests I and II. Total copper in samples containing >200 μg Cu/l was determined by direct aspiration of seawater into the flame of a Model 303 Perkin Elmer[10] atomic absorption spectrophotometer (AAS) with a deuterium background corrector; total copper in samples containing <200 and >10 μg Cu/l was determined by direct injection of a sample aliquot into an HGA 2100 model graphite furnace after 1:1 dilution of the sample with ultrapure 2 N HNO_3. Labile copper, defined operationally as that fraction passing through a 0.45 μm filter and retained by NH_4-Chelex resin, was determined by the method of Riley and Taylor (1968). Eluants from the columns were analyzed directly in the flame or in the graphite furnace of the AAS.

The mean total copper concentrations measured during each test are given in Tables 1 and 2. The percentage of the total copper in the labile form for all concentrations averaged 96% (SD = ±2.60). The mean pH of the exposure seawater for all tests was 8.06 (SD = ±0.05).

The primary measure of toxicity for this study was the copper concentration resulting in 50% mortality over a given time (median lethal concentration, LC_{50}). This toxicity measure was determined by performing weighted least squares estimates and maximum likelihood estimates for the parameters $\propto$ and β in the logit model:

$$P(x) = \frac{e^{\propto + \beta x}}{1 + e^{\propto + \beta x}}.$$

The linear transform of the logistic function is $\text{logit}\, P = \ln P(x)/1-P(x) = \propto + \beta x$; thus if logit P is plotted against x, the points should fall on a straight line with $\propto$ as the intercept and β as the slope (Berkson 1953). The weighted least squares estimates for $\propto$ and β were found first and then used as the initial estimates for the maximum likelihood estimates (Koshiver and Moore 1979).

In our calculation of LC_{50}, $P(x)$ is the proportion responding at dose x. Our method followed that outlined by the American Public Health Association (1976) except that the logit analysis was used in place of a probit analysis. For each observation time, an estimated LC_{50} value was determined. The series of LC_{50} values obtained were used to construct a toxicity curve that was used to estimate the incipient lethal concentration (lethal threshold concentration, ILC_{50}; Sprague 1969).

RESULTS

Northern anchovy embryos continuously exposed to copper showed high mortality during the first 8-10 h of exposure (Table 1). After 10 h, the mortality rate was relatively constant until hatching (Figures 2-4). The embryos took two different forms at mortality. The first form (Type I) was observed predominantly during the initial 8-10 h of exposure and accounted for varying proportions of the total mortality, depending on the copper exposure concentration (Table 3). These embryos appeared to have had epiboly disrupted; the yolk was naked and a deformed opaque mass of protoplasm was found at the animal pole. The second form (Type II) appeared similar to normally developing embryos (the embryo encircling the yolk sac), except for an opacity of the embryo. In em-

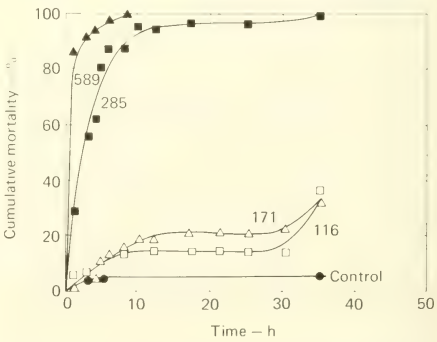


FIGURE 2.—Percentage cumulative mortality of northern anchovy embryos continuously exposed to copper during test I: numbers next to curves are the exposure concentrations in μg Cu/l.

[10]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA, or the University of California.

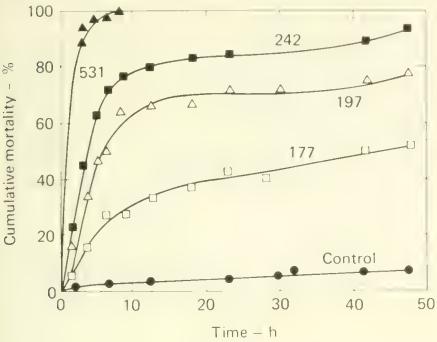


FIGURE 3.—Percentage cumulative mortality of northern anchovy embryos continuously exposed to copper during test II: numbers next to curves are the exposure concentrations in μg Cu/l.

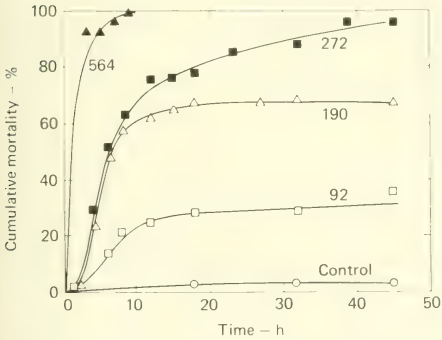


FIGURE 4.—Percentage cumulative mortality of northern anchovy embryos continuously exposed to copper during test III: numbers next to curves are the exposure concentrations in μg Cu/l.

TABLE 3.—Types of mortality and the percentage hatching of northern anchovy embryos exposed to different concentrations of copper.

Mean Cu concentration (μg l)	Tests pooled	Embryos showing type of mortality (%)		Hatching (%)
		Type I[1]	Type II[2]	
Control	I, III	3	4	93
92	III	4	32	64
177	II	34	20	46
194	II, III	63	17	20
257	II, III	60	35	5
548	II, III	96	2	2

[1]Epiboly disrupted, the yolk naked and a deformed opaque mass of protoplasm at the animal pole.
[2]Dead after epiboly, embryo appears normally developed.

bryos with either type of mortality the chorion was clear at the time the embryos were removed from the exposure chambers. However, during preliminary testing, we noted that the chorion became opaque when dead embryos were allowed to remain in copper concentrations as low as 100 μg Cu/l for a period of time. Embryo mortalities of both types were found at the bottom of the exposure chambers whereas normal embryos were found at or near the surface of the water, except just before hatching when they tended to sink. The estimated mean hatching time from the start of copper exposure was 32, 33, and 37 h for embryo tests I, II, and III, indicating that in each test the embryos were exposed during similar developmental periods. Hatching success was high for controls and decreased with increases in copper exposure concentration.

Larval control mortalities were high, but followed the general pattern for larvae not fed during yolk-sac absorption (O'Connell and Raymond 1970; Lasker et al. 1970). Northern anchovy larvae continuously exposed to concentrations <200 μg Cu/l consistently showed better survival than did the controls (Table 3) (Figures 5, 6). Though he offered no explanation, Benoit (1975) found bluegill, *Lepomis macrochirus*, larval survival greater at 12 μg Cu/l than in the controls. It is possible that low levels of copper exposure increased survival of both the northern anchovy and bluegill larvae by inhibiting harmful microbial populations. The period of yolk absorption was estimated to be between 24 and 30 h from the start

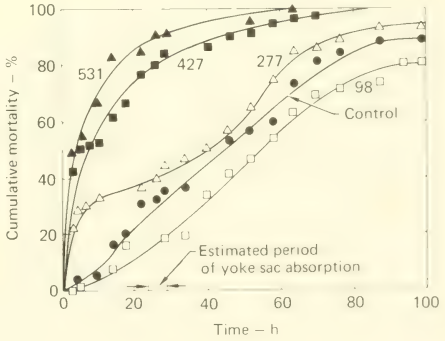


FIGURE 5.—Percentage cumulative mortality of northern anchovy larvae continuously exposed to copper during test I: numbers next to curves are the exposure concentrations in μg Cu/l.

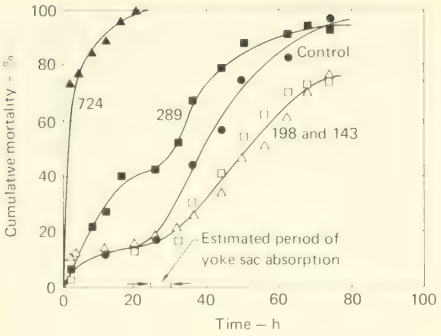


FIGURE 6.—Percentage cumulative mortality of northern anchovy larvae continuously exposed to copper during test II: numbers next to curves are the exposure concentrations in μg Cu/l.

of larval exposure. During exposures >200 μg Cu/l, synergism between copper toxicity and starvation may have played a role in the mortality and the shape of the 277 and 289 μg Cu/l mortality curves (Figures 5, 6) may show this effect.

No obvious abnormalities were noted in the dead larvae. Before death, larvae tended to sink to the bottom of the exposure chambers and often exhibited head shaking movements and whip movements in which head and tail met.

Examples of the cumulative mortality data used to calculate LC_{50} values and to generate the toxicity curves (Figure 7) are given in Tables 1 and 3. Chi-square values for embryo cumulative mortality curves at every observation time were significant. This variation from the logit model may possibly be due to changes in copper sensitivity as the embryos developed. Chi-square values for larval cumulative mortality curves at different observation times indicate a better fit to the logit model.

The embryonic and larval toxicity curves reflect several developmental changes in sensitivity (Figure 7). A slight increase in copper sensitivity can be seen in the embryos during hatching. When we estimated the embryo ILC_{50}, we considered only mortalities before hatching. For embryos, the estimated ILC_{50} was found to be 190 μg Cu/l, and was reached approximately 24 h after the start of copper exposure. The sudden increase in mortality of the larvae at about 40 h probably was the result of starvation. Only mortalities before this time were considered in the larval estimated ILC_{50}. The ILC_{50} for the northern anchovy larvae was found to be higher than for embryos: 370 μg Cu/l copper, and was reached about 32 h after the start of copper exposure. The estimated 24-h LC_{50} was 398 μg Cu/l.

DISCUSSION

We found the embryonic stage of the northern anchovy to be more sensitive to copper than the larval stage. This is in keeping with the majority

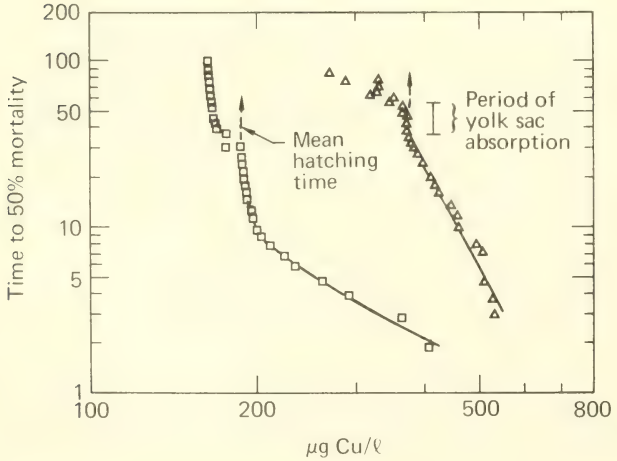


FIGURE 7.—Toxicity curves for nothern anchovy embryos and larvae continuously exposed to copper.

of previous studies examining the sensitivity to copper of marine fishes' early life history stages (Engle et al. 1976; Blaxter 1977; Rice and Harrison 1978). In contrast, studies examining the copper sensitivity of various life stages of freshwater fishes revealed that the larval stages are the most sensitive to copper (Hazel and Meith 1970; McKim and Benoit 1971; Gardner and LaRoche 1973; Benoit 1975; McKim et al. 1978; O'Rear[11]). This difference in comparative sensitivity between embryos and larvae of freshwater and marine fishes suggests that caution should be exercised in applying the extensive results of toxicity tests on freshwater fishes to marine fishes.

The adult northern anchovy and Pacific herring are similar in form and in behavior, but their reproductive strategies are quite different. The northern anchovy spawns pelagic eggs into offshore waters; the 1.0 × 0.5 mm diameter egg is covered by an elliptical, transparent chorion. Northern anchovy eggs hatch in about 48 h at 17° or 18° C into fragile, unpigmented larvae, 2.5-3.0 mm long (Ahlstrom 1956). The Pacific herring spawns demersal, adhesive eggs on shallow intertidal substrates; the 1.3-1.6 mm diameter egg is covered by a thick, three-layered, chorion (Blaxter and Holliday 1963). Herring eggs hatch in 7-9 d at 14° C into pigmented larvae 5.0-6.0 mm long (Alderdice and Velsen 1971). Comparisons of the sensitivities of the early life stages of these two fish may prove useful for predicting the impact of copper on broad groups of fishes. For comparisons between the copper sensitivity of northern anchovy and Pacific herring embryos and larvae, the data on herring sensitivity are taken from our earlier study (Rice and Harrison 1978).

It might be expected that the fragile northern anchovy embryo would be more sensitive to copper than the larger, tougher Pacific herring embryo; in fact, however, the opposite appears to be the case. The ILC_{50} for northern anchovy embryos was approximately six times higher than that for Pacific herring embryos. The results of Engel and Sunda (1979) showed a similar pattern; relatively tough benthic spawned eggs of the silverside, *Menidia menidia*, were found to be more sensitive to copper than the more fragile pelagic eggs of the spot.

The differences in sensitivity seen in the two embryos may be the result of differences in the chorionic structure and the developmental period during copper exposure. The chorion of Atlantic herring, *C. h. harengus* (Rosenthal and Sperling 1974), and another demersal adhesive egg, the Baltic garpike, *Belone belone* (Dethlefsen et al. 1975), have been shown to concentrate cadmium. The chorion of the Pacific herring may be the site of mechanisms to accumulate metals, mechanisms that may be reduced or lacking in the northern anchovy. Changes in sensitivity during development were seen in both the northern anchovy and Pacific herring embryos. The high percentage of northern anchovy mortalities during epiboly indicates that this period of development might be more sensitive to copper than the later developmental periods. Increased copper sensitivity during this period also was found for winter flounder, *Pseudopleuronectes americanus*, (Cardin[12]). The sensitive period for the Pacific herring embryo appeared to be about 96 h after fertilization, well beyond epiboly.

Differences in sensitivity were also seen between the two larvae. The fragile northern anchovy larvae were about three times more sensitive to copper than the Pacific herring larvae.

Both northern anchovy and Pacific herring larvae displayed spasms before death at the higher copper concentrations to which they were exposed. Such spasms during copper poisoning have been suggested to be similar to those seen in Wilson's Disease (Baker 1969).

ACKNOWLEDGMENTS

The authors thank Revelle Davis, John Dawson, and Rose Carrillo for their assistance in the collection, handling, and observation of the test organisms.

This work was supported by the U.S. Nuclear Regulatory Commission under a Memorandum of Understanding with the U.S. Department of Energy.

LITERATURE CITED

AHLSTROM, E. H.
1943. Appendix. *In* Studies on the Pacific pilchard or sardine (*Sardinops caerulea*). 4.—Influence of temperature

[11]O'Rear, C. W., Jr. 1972. The toxicity of zinc and copper to striped bass eggs and fry with methods for providing confidence limits. Southeast. Assoc. Game Fish Comm., 26th Annu. Conf., p. 484.

[12]Cardin, J. 1976. *In* Annual Report, January-December 1976. U.S. Environ. Prot. Agency, Environ. Res. Lab., Narragansett, R.I., 42 p.

on the rate of development of pilchard eggs in nature, p. 9-12. U.S. Fish Wildl. Serv., Spec. Sci. Rep. 23.

1956. Eggs and larvae of anchovy, jack mackerel, and Pacific mackerel. Calif. Coop. Oceanic Fish. Invest. Prog. Rep. 1 April 1955 to 30 June 1956, p. 33-42.

1960. Vertical distribution of pelagic fish eggs and larvae off California and Baja California. U.S. Fish Wildl. Serv., Fish. Bull. 60:107-146.

ALDERDICE, D. F., AND F. P. J. VELSEN.

1971. Some effects of salinity and temperature on early development of Pacific herring (*Clupea pallasi*). J. Fish. Res. Board Can. 28:1545-1562.

AMERICAN PUBLIC HEALTH ASSOCIATION.

1976. Standard methods for the examination of water and wastewater. 14th ed. Am. Public Health Assoc., Am. Water Works Assoc., Water Pollut. Control Fed., Wash., D.C., 1193 p.

ANONYMOUS.

1972. Water quality control plan for ocean waters of California. California State Water Resources Control Board, 13 p.

1976. Ocean plan review status report. California State Water Resources Control Board, 19 p.

BAKER, J. T. P.

1969. Histological and electron microscopical observations on copper poisoning in the winter flounder (*Pseudopleuronectes americanus*). J. Fish. Res. Board Can. 26:2785-2793.

BATLEY, G. E., AND T. M. FLORENCE.

1976. Determination of the chemical forms of dissolved cadmium, lead and copper in seawater. Mar. Chem. 4:347-363.

BECKER, C. D., AND T. O. THATCHER.

1973. Toxicity of power plants chemicals to aquatic life. Publ. WASH-1249, U.S. At. Energy Comm., 222 p.

BENOIT, D. A.

1975. Chronic effects of copper on survival, growth, and reproduction of the bluegill (*Lepomis macrochirus*). Trans. Am. Fish. Soc. 104:353-358.

BERKSON, J.

1953. A statistically precise and relatively simple method of estimating the bio-assay with quantal response, based on the logistic function. J. Am. Stat. Assoc. 48:565-599.

BLAXTER, J. H. S.

1977. The effect of copper on the eggs and larvae of plaice and herring. J. Mar. Biol. Assoc. U.K. 57:849-858.

BLAXTER, J. H. S., AND F. G. T. HOLLIDAY.

1963. The behaviour and physiology of herring and other clupeids. Adv. Mar. Biol. 1:261-393.

CUSHING, D. H.

1975. Marine ecology and fisheries. Camb. Univ. Press, Camb., Engl., 278 p.

DAVEY, E. W., M. J. MORGAN, AND S. J. ERICKSON.

1973. A biological measurement of the copper complexation capacity of seawater. Limnol. Oceanogr. 18:993-997.

DETHLEFSEN, V., H. VON WESTERNHAGEN, AND H. ROSENTHAL.

1975. Cadmium uptake by marine fish larvae. Helgol. wiss. Meeresunters. 27:396-407.

ENGEL, D. N., AND W. G. SUNDA.

1979. Toxicity of cupric ion to eggs of the spot, *Leiostomus xanthurus* and the Atlantic silverside *Menidia menidia*. Mar. Biol. (Berl.) 50:121-126.

ENGEL, D. W., W. G. SUNDA, AND R. M. THUOTTE.

1976. Effects of copper on marine fish eggs and larvae. Environ. Health Perspect. 17:288-289.

GARDNER, G. R., AND G. LAROCHE.

1973. Copper induced lesions in estuarine teleosts. J. Fish. Res. Board Can. 30:363-368.

HAZEL, E. R., AND S. J. MEITH.

1970. Bioassay of king salmon eggs and sac fry in copper solutions. Calif. Fish Game 56:121-124.

KOSHIVER, J., AND D. MOORE.

1979. Logit: A program for dose-response analysis. Comp. Prog. Biomed. 10:61-65.

LASKER, R., H. M. FEDER, G. H. THEILACKER, AND R. C. MAY.

1970. Feeding, growth, and survival of *Engraulis mordax* larvae reared in the laboratory. Mar. Biol. (Berl.) 5:345-353.

LEE, F. G.

1973. Review paper. Chemical aspects of bioassay techniques for establishing water quality criteria. Water Res. 7:1525-1546.

LEWIS, A. G., P. H. WHITFIELD, AND A. RAMNARINE.

1972. Some particulate and soluble agents affecting the relationship between metal toxicity and organism survival in the calanoid copepod *Euchaeta japonica*. Mar. Biol. (Berl.) 17:215-221.

1973. The reduction of copper toxicity in a marine copepod by sediment extract. Limnol. Oceanogr. 18:324-326.

MARTIN, M., M. D. STEPHENSON, AND J. H. MARTIN.

1977. Copper toxicity experiments in relation to abalone deaths observed in a power plant's cooling waters. Calif. Fish Game 63:95-100.

MAY, R. C.

1974. Larval mortality in marine fishes and the critical period concept. *In* J. H. S. Blaxter (editor), The early life history of fish, p. 3-19. Springer-Verlag, N.Y.

MCALLISTER, R.

1976. California marine fish landings for 1974. Calif. Dep. Fish Game, Fish Bull. 166, 53 p.

MCKIM, J. M., AND D. A. BENOIT.

1971. Effects of long-term exposures to copper on survival, growth, and reproduction of brook trout (*Salvelinus fontinalis*). J. Fish. Res. Board Can. 28:655-662.

MCKIM, J. M., J. G. EATON, AND G. W. HOLCOMBE.

1978. Metal toxicity to embryos and larvae of eight species of freshwater fish - II: copper. Bull. Environ. Contam. Toxicol. 19:608-616.

NEFF, J. M., AND J. W. ANDERSON.

1977. The effects of copper (II) on molting and growth of juvenile lesser blue crabs *Callinectes similis* Williams. *In* C. S. Giam (editor), Pollutant effects on marine organisms, p. 155-159. Lexington Books, Lexington, Mass.

O'CONNELL, C. P., AND L. P. RAYMOND.

1970. The effect of food density on survival and growth of early post yolk-sac larvae on the northern anchovy (*Engraulis mordax* Girard) in the laboratory. J. Exp. Mar. Biol. Ecol. 5:187-197.

PAGENKOPF, G. K., R. C. RUSSO, AND R. V. THURSTON.

1974. Effect of complexation on toxicity of copper to fishes. J. Fish. Res. Board Can. 31:462-465.

PINKAS, L.

1977. California marine fish landings for 1975. Calif. Dep. Fish Game, Fish Bull. 168, 55 p.

RICE, D. W., JR., AND F. L. HARRISON.

1978. Copper sensitivity of Pacific herring, *Clupea haren-*

gus pallasi, during its early life history. Fish. Bull., U.S. 76:347-356.

RILEY, J. P., AND D. TAYLOR.
1968. Chelating resins for the concentration of trace elements from sea water and their analytical use in conjunction with atomic absorption spectrophotometry. Anal. Chim. Acta 40:479-485.

ROSENTHAL, H., AND K.-R. SPERLING.
1974. Effects of cadmium on development and survival of herring eggs. *In* J. H. S. Blaxter (editor), The early life history of fish, p. 383-396. Springer-Verlag, N.Y.

SPRAGUE, J. B.
1969. Measurement of pollutant toxicity to fish. I. Bioassay methods for acute toxicity. Water Res. 3:793-821.

SUNDA, W., AND R. R. L. GUILLARD.
1976. The relationship between cupric ion activity and the toxicity of copper to phytoplankton. J. Mar. Res. 34:511-529.

VAUGHAN, D. S., AND S. B. SAILA.
1976. A method for determining mortality rates using the Leslie matrix. Trans. Am. Fish. Soc. 105:380-383.

CHANGES IN BODY MEASUREMENTS OF LARVAL NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, AND OTHER FISHES DUE TO HANDLING AND PRESERVATION

GAIL H. THEILACKER[1]

ABSTRACT

The relation between northern anchovy length and body parts was compared for live and laboratory-preserved larvae as well as larvae treated in a net to simulate field collection conditions. Larvae were damaged by net abrasion, and those netted before preservation shrank more than those that were laboratory preserved (that is, larvae pipetted directly into preservative). Shrinkage of net-treated individuals decreased with age and increased with handling time, but shrinkage of laboratory-preserved larvae was constant for the size class studied. The results show that morphological differences reported for laboratory-reared and sea-caught larvae of the same length may result from the method of handling larvae prior to preservation.

To describe life stages of larval fish, field and laboratory studies rely on length measurements of preserved sea-collected and preserved laboratory-collected larvae. Sea-collected larvae incur mechanical damage, abrasion from the collecting net and from other plankters, while the net is being towed and washed down (Ahlstrom 1976). When damaged, delicate larvae shrink. This initial shrinkage usually occurs before death, and this shrinkage is compounded by preservative shrinkage (Blaxter 1971). Conversely, laboratory handling of larvae prior to preservation is less damaging than net abrasion. In the laboratory, individual larvae are usually transferred by pipette or beaker to preservative, and they die and shrink in the preservative.

Laboratory-reared fish larvae differ morphologically from sea-caught larvae. Body depth of wild herring, *Clupea harengus*, larvae was smaller than that of starved laboratory-reared larvae of the same preserved length (Blaxter 1971). Ryland (1966) observed that sea-sampled larval plaice, *Pleuronectes platessa*, were smaller than laboratory larvae at a comparable stage and suggested that a factor for shrinkage was needed to equate field with laboratory measurements. I have noticed a similar discrepancy in preserved length of sea-collected yolk-sac larvae and laboratory-hatched and preserved yolk-sac larvae of the jack mackerel, *Trachurus symmetricus* (Theilacker unpubl. data). These morphological differences may be the result of the method of handling (laboratory capture or net capture) prior to preservation. Since it is necessary to compare animals at the same developmental stage to relate laboratory larval fish studies to the field, there is a need to intercalibrate field (preserved) and laboratory (live and preserved) larval fish measurements.

METHODS

Adult northern anchovy, *Engraulis mordax*, maintained in the Southwest Fisheries Center's aquarium, were spawned by hormone injection (Leong 1971). I reared the anchovy larvae at 15.5° C on cultured food organisms (*Gymnodinium splendens*; rotifers, *Brachionus plicatilis*; and copepods, *Tisbe furcata*) in 100 l tanks using methods described by Lasker et al. (1970), Theilacker and McMaster (1971), and Hunter (1976).

I considered several factors that could affect shrinkage of larval fish: 1) size, 2) type of fixative, 3) treatment of larvae before fixation (net or laboratory capture), and 4) duration of net retention. Larval fish measurements fit into four treatment categories (Figure 1): 1) live, 2) laboratory pipetted and preserved, 3) net treated, and 4) preserved after net treatment (equivalent to "field-collected" larvae). Five body measurements (in millimeters) were taken: standard length (SL), tip of upper jaw to perpendicular at end of notochord; head length, tip of upper jaw to cleithrum; body depth at the pectoral (not measured

[1]Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

Manuscript accepted January 1980.
FISHERY BULLETIN: VOL. 78, NO. 3, 1980.

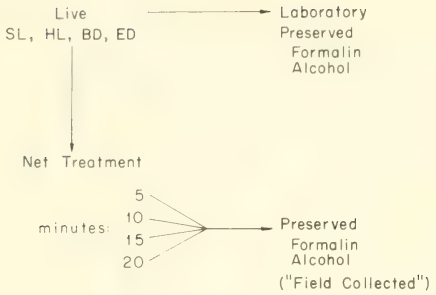


FIGURE 1.—Experimental design. Four measurements of larval northern anchovy were taken to estimate shrinkage during handling treatments: standard length, SL; head length, HL; body depth at the anus, BD; and eye diameter, ED.

for northern anchovy); body depth at the anus; and eye diameter. I kept track of individual larvae during all treatments and determined body part shrinkage on an individual basis. The same larva could be measured as many as six times; e.g., a "field-collected" larva was measured live, after four time intervals in the net, and again after preservation. However, not all net-treated larvae were measured for four time intervals. I used several preservatives: Bouin's fixative, usually used for histological studies; 5% buffered Formalin[2] (2.2% formaldehyde), the standard ichthyoplankton-survey preservative (Ahlstrom 1976; Smith and Richardson 1977); and 80% ethyl alcohol, preservative for otoliths (Methot and Kramer 1979). In treatments (2) and (4), larvae were kept in preservative for 4-5 wk before remeasuring.

As an example of laboratory handling procedures, I have included results from ongoing studies on morphology of jack mackerel and Pacific barracuda, *Sphyraena argentea*, larvae. Eggs of jack mackerel and Pacific barracuda were collected 30-50 km off the coast of southern California in June and July 1977, and rearing procedures were the same as for northern anchovy. Laboratory handling in this study consisted of pipetting live larvae 1) onto a slide for measurement and 2) into preservative. Time spent handling was an important factor affecting shrinkage. Larvae shrink during the measuring process. In this study, all live and laboratory shrinkage measurements include about a 30 s handling time. Some scientists measure laboratory-reared larvae only after preservation; these larvae are probably handled <30 s.

In his paper on the quality of field-collected fish larvae, Ahlstrom (1976) noted several conditions that damaged specimens: fast net speeds, high temperatures, and increased time in the net. During standard ichthyoplankton surveys, larvae in the nets could be damaged by abrasion for up to 20 min before preservation, the net is towed for 20 min, ascending 15 min, and then the collected sample is washed down into the cod end and preserved (Ahlstrom 1976; Smith and Richardson 1977). Considering these variables, I designed a net treatment to simulate shipboard procedures. For the treatment, seawater was circulated over a single larva in a submerged net container. (Small larvae, 4-7 mm, were treated in groups of 10.) To obtain conservative results, the water temperature was cool, 13° C, and the net-treatment time varied: 5, 10, 15, and 20 min. The net-treatment time included the pipetting and measuring as well as the time in the net. After net treatment, larvae were preserved; I equate these net-treated and preserved larvae with field-collected larvae (Figure 1).

RESULTS

Live Body Parts

Head length, body depth, and eye diameter were examined as functions of standard length for live northern anchovy larvae (Figure 2, Table 1). On a double logarithmic scale (Figure 2) both head length and body depth relationships show curvature, but the eye diameter relation appears to be nearly linear. According to Zweifel,[3] the simple allometric body part relationships used for juvenile and adult fish are not adequate for describing body part relationships of larval fish, except for very limited ranges of size or age. Therefore, I assumed that the larval body proportions (y) change continuously during growth, varying according to a nonlinear allometric growth model,

$$\ln y = a - b(c - \ln x)^d,$$

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[3]Zweiful, J. T. Equations of growth and allometry in larval and adult fish. Unpubl. manuscr. Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

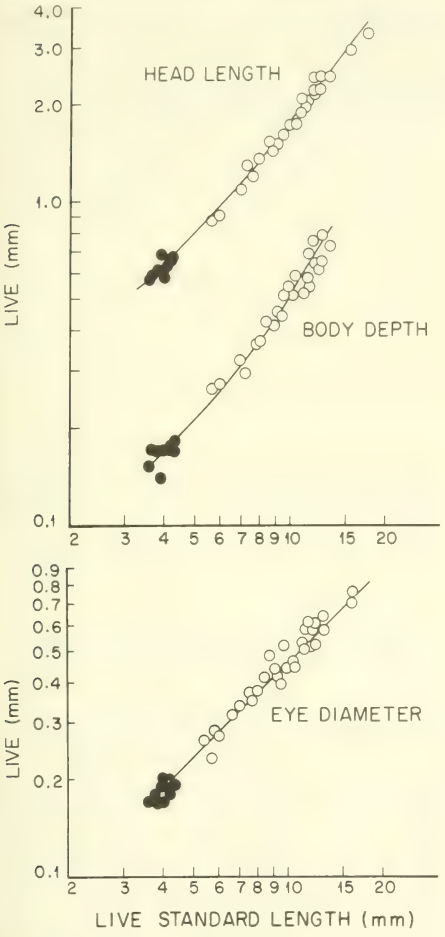


FIGURE 2.—Head length, body depth, and eye diameter as functions of standard length in live northern anchovy larvae. Nonlinear models for live head length and body depth with standard lengths and linear model for eye diameter with standard length are described in the text; estimated parameters are in Table 1. Dots are means of 10 larvae. Circles represent individual fish.

obtained by eliminating time (t) from two Gompertz equations

$$y = y_0 \exp(A_0[1-\exp(-\alpha t)]/\alpha) \text{ and}$$
$$x = x_0 \exp(B_0[1-\exp(-\beta t)]/\beta)$$

TABLE 1.—Estimated parameters for nonlinear and linear models relating live body part measurements (y) with standard length (x) of northern anchovy larvae.

y	n	a	b	c	d
Head length[1]	86	4.120	2.456	4.189	0.607
Body depth[1]	38	2.922	3.699	3.241	0.389
Eye diameter[2]	44	−3.021	0.976		

[1] $\ln y = a - b \ln(c - \ln x^d)$
[2] $\ln y = a + b \ln x$

(Zweifel footnote 3). a corresponds to the natural logarithm of the asymptotic size of y; c represents the natural logarithm of the asymptotic size of x (standard length); and d is the ratio of the decay parameters α and β in the individual Gompertz growth curves. The parameter b has no simple biological interpretation except when the decay parameters are equal ($d = 1$); in this case the equation is reduced to a simple allometric growth model. The model was fit to the observed head length and body depth measurements using Marquardt's algorithm for fitting nonlinear models (Conway et al. 1970). The equations (Table 1) gave a good fit to the data (Figure 2). The relation between eye diameter and all treatments is discussed in the section on Eye Diameter.

Laboratory Shrinkage

For northern anchovy larvae preserved in Formalin, the ratio of preserved to preceding live size for standard length (Figure 3), head length, and body depth did not increase with length; i.e., shrinkage did not decrease with age. The ratio averaged 0.92 for standard length after shrinkage in Formalin, and this relation also held for shrinkage in standard length of northern anchovy, jack mackerel, and Pacific barracuda larvae preserved in Bouin's fixative (Table 2). Shrinkage of other body parts differed among species, but the measurements were not made on all three species in

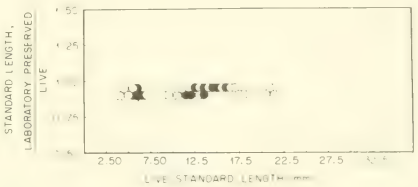


FIGURE 3.—Ratio of subsequent laboratory-preserved standard length to live standard length in northern anchovy preserved in Formalin. Dots are means of two or three larvae. Circles represent individual fish.

TABLE 2.—Shrinkage of laboratory-preserved northern anchovy, jack mackerel, and Pacific barracuda. Ratio is laboratory-preserved size divided by previous live size (1.00 = no shrinkage). Standard length; head length; eye diameter; body depth at the pectoral, BD-1; and body depth at the anus, BD-2. Measurements in millimeters.

		Standard length				Head length				Eye diameter			BD-1			BD-2		
Species	Fixative	No	Range	Ratio	SD	No	Range	Ratio	SD	Range	Ratio	SD	Range	Ratio	SD	Range	Ratio	SD
Northern anchovy	Formalin	61	3.9 -21.6	0.92	0.03	23	0.58-2.41	0.91	0.07	0.17-0.61	1.05	0.08	—	—	—	0.14-0.82	0.90	0.10
	Alcohol	26	3.7 -19.0	1.00	.04	—	—	—	—	—	—	—	—	—	—	—	—	—
	Bouins[1]	224	3.8 -15.7	.92	.00	—	—	—	—	—	—	—	—	—	—	—	—	—
Jack mackerel	Bouins	45	3.25-3.90	.92	.03	43	0.74-0.97	.82	.04	0.26-0.33	.90	.06	0.48-0.67	0.75	0.05	0.20-0.26	.75	.05
Pacific barracuda	Bouins	54	3.75-5.23	.92	.02	56	1.00-1.63	.79	.05	0.30-0.48	.82	.04	0.58-0.96	.75	.04	0.24-0.41	.77	.05

[1]P. Paloma, Fishery Biologist, National Marine Fisheries Service, La Jolla, Calif. Unpubl. data.

the same preservative. Jack mackerel and Pacific barracuda, deeper bodied than northern anchovy at the same length, were preserved in Bouin's fixative, and northern anchovy were preserved in Formalin. Head length, eye diameter, and body depth shrank more in jack mackerel and Pacific barracuda larvae than in northern anchovy larvae (Table 2). Eye diameter of northern anchovy increased in size after Formalin preservation; the increase was significant ($P = 0.058$; paired t-test) but small (0.0145±0.0031 mm).

Alcohol preservation did not cause a change in northern anchovy standard length (Figure 4, Table 2); smaller body parts were not measured because alcohol distorted the larvae and they were extremely difficult to remeasure after preservation.

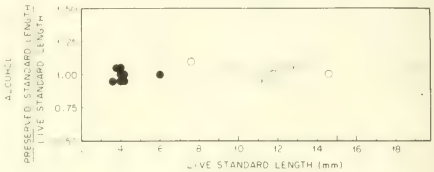


FIGURE 4.—Ratio of subsequent laboratory-preserved standard length to live standard length in northern anchovy preserved in alcohol. Dots are means of 10 larvae. Circles represent individual fish.

Net-Treatment Shrinkage

Shrinkage of net-treated larval northern anchovy varied with handling time and fish size (Ta-

TABLE 3.—Shrinkage in standard length (millimeter) of northern anchovy larvae after net handling for four time intervals (X_2). Ratio (R) = mean net standard length (X_1) divided by mean live standard length (L). Ratio of 1.00 = no shrinkage.

		Mean size		Ratio			Mean size		Ratio	
Live size	n	Live	5 min net	Observed	Estimated[1]	n	Live	10 min net	Observed	Estimated[1]
4.00- 5.99	3	4.27	3.46	0.81	0.84	8	4.40	3.55	0.81	0.81
6.00- 7.99	3	7.57	6.87	0.91	0.90	9	7.17	5.99	0.84	0.85
8.00- 9.99	5	9.02	8.16	0.90	0.92	11	8.87	7.71	0.87	0.87
10.00-11.99	9	10.98	10.21	0.93	0.94	21	11.11	9.85	0.89	0.89
12.00-13.99	6	12.63	12.12	0.96	0.95	29	12.90	11.58	0.90	0.90
14.00-15.99	6	14.60	13.83	0.95	0.96	18	14.85	13.45	0.91	0.92
16.00-17.99	2	16.70	15.80	0.95	0.97	11	16.65	15.22	0.91	0.93
18.00-19.99	4	19.20	18.73	0.98	0.98	11	18.93	17.71	0.94	0.94
20.00-21.99	3	21.10	20.67	0.98	0.99	7	20.80	19.71	0.95	0.95
22.00-23.99	—	—	—	—	—	2	22.75	21.50	0.95	0.96
24.00-25.99	1	24.70	24.50	0.99	0.99	2	24.85	24.10	0.97	0.97
26.00-27.99	1	26.70	26.00	0.97	0.99	1	26.70	25.50	0.96	0.97

		Mean size		Ratio			Mean size		Ratio	
Live size	n	Live	15 min net	Observed	Estimated[1]	n	Live	20 min net	Observed	Estimated[1]
4.00- 5.99	2	4.22	3.41	0.81	0.80	—	—	—	—	—
6.00- 7.99	2	7.35	6.20	0.84	0.83	1	7.50	6.50	0.87	0.82
8.00- 9.99	4	8.96	7.55	0.84	0.84	—	—	—	—	—
10.00-11.99	5	11.44	9.84	0.86	0.86	3	11.73	10.30	0.88	0.85
12.00-13.99	4	12.85	11.29	0.88	0.88	1	13.70	11.50	0.84	0.86
14.00-15.99	7	14.57	12.73	0.87	0.89	6	14.60	12.55	0.86	0.87
16.00-17.99	4	16.57	14.53	0.88	0.90	2	16.70	14.30	0.86	0.88
18.00-19.99	5	19.22	17.72	0.92	0.92	5	19.22	17.22	0.90	0.90
20.00-21.99	3	21.10	19.67	0.93	0.93	3	21.10	19.37	0.92	0.91
22.00-23.99	1	23.50	21.40	0.91	0.94	1	23.50	21.40	0.91	0.92
24.00-25.99	1	24.70	23.40	0.95	0.94	1	25.00	23.80	0.95	0.93
26.00-27.99	1	26.70	24.60	0.92	0.95	—	—	—	—	—

[1]Estimated ratio = $\ln X_1 - \ln L$; Equation (4), see text and Table 4.

ble 3). In larvae 6 mm SL or less, maximum shrinkage (19%) occurred after 5-10 min treatment in the net; larvae were usually dead at the end of the treatment. Older larvae shrank throughout the 20-min period and were often alive at the end. For example, 18-22 mm larvae were 2% smaller after 5 min and 8-10% smaller after 20 min in the net. Further net treatment of larger larvae caused an additional 1-2% shrinkage. Figure 5

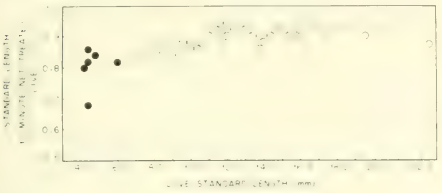


FIGURE 5.—Ten-minute net-treated shrinkage of standard length as a function of size for northern anchovy larvae. Dots are means of 10 larvae. Circles represent individual fish.

shows that measurable shrinkage decreases for older, larger larvae, and that the ratio (R) of the size of net-treated (X_1) to live (L) size larvae rises rapidly from about 0.7-0.8 at 4 mm SL to 0.9 by 11-12 mm SL. Although shrinkage appears nearly constant for larvae from 12 to 22 mm (Figure 5), I measured few older, larger larvae. Conceptually, shrinkage is probably related to the degree of ossification; ossification of northern anchovy vertebrae begins at 14 mm SL and is complete at transformation, about 35 mm (E. H. Ahlstrom[4]). At transformation, shrinkage should be negligible or zero, and the ratio should approach an asymptote of one. To characterize this relationship, I used the equation

$$R = \exp[(-f_1)\exp(-f_2 X_1)]. \quad (1)$$

Equation (1) may be transformed so that the double logarithm of R is a linear function of size, X_1, i.e.

$$\ln[-\ln(R)] = \ln f_1 - f_2 X_1. \quad (2)$$

For standard length measurements, the parameters of Equation (2) were estimated for each of the four net-treatment periods as shown below:

Net-treatment time = t	$\ln f_1$	f_2
5	−1.3436	0.1209
10	−1.2708	0.0752
15	−1.2479	0.0509
20	−1.3759	0.0430

The logarithm of f_2 is linear with net-treatment time, i.e.

$$f_2 = g_1 t^{g_2}, \quad (3)$$

while f_1 shows no trend. Combining these two relationships, i.e., R with size (Equation (1)) and f_2 with time (Equation (3)), and inverting the equation to solve for live size in terms of treated larvae, the resultant relationship is

$$\ln L = \ln X_1 + P_1 \exp(-P_2 X_1 X_2^{P_3}) \quad (4)$$

where L is live size, $P_1 = f_1, P_2 = f_1 g_1, P_3 = g_2$, X_1 is treated size, and X_2 is time (t) in minutes. Equation (4) was then fit directly using a nonlinear fitting procedure (Conway et al. 1970) to obtain the final parameter estimates. The same procedure for estimating parameters and fitting equations was followed for shrinkage of head length and body depth. All equations gave a good fit to the observed data (Figure 6, Table 3); estimates of the parame-

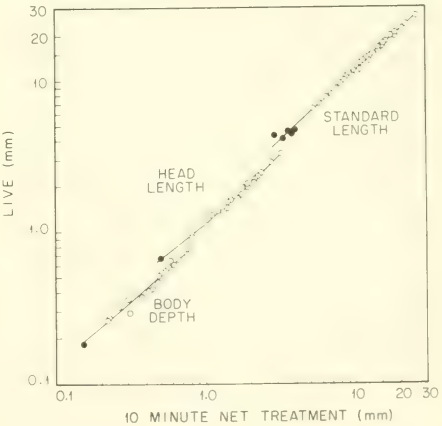


FIGURE 6.—Fit of models (Equation (4)) describing net-treatment shrinkage of larval northern anchovy body parts. Estimates of parameters for models are given in Table 4. Models predict live size from net-treated size.

[4]E. H. Ahlstrom, Senior Scientist, Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun. December 1978.

TABLE 4.—Estimated parameters for models that predict live northern anchovy body part size (L) from net-treated size (X_1).

Model[1]	P_1	P_2	P_3
Standard length	0.289	0.434	0.680
Head length	0.177	3.858	−0.605
Body depth	0.413	29.746	−0.620

[1]Equation (4), see text.

ters for the standard length, head length, and body depth models are given in Table 4. These equations can be used to estimate live size of each body part from measurements of northern anchovy larvae after net capture.

Preservation Shrinkage (After Net Treatment)

After larvae shrank during net treatment, additional shrinkage caused by Formalin was nearly a constant proportion of length (Figure 7). The ratio of preserved length to net-treated length (Figure 7) may decrease slightly (i.e., shrinkage may increase) with increasing fish size, but this slight decrease has no practical significance for length calibration of larvae taken in routine plankton samples. Because ossification begins at 14 mm SL, I expect large fish would shrink less, not more, than small fish. The overall mean ratio (preserved size/size after each timed-net treatment) of 104 standard length measurements was 0.9668± 0.0020; percent shrinkage of the other body parts was the same as standard length shrinkage. I recommend using 3% shrinkage for all body parts in Formalin after net treatment. Preservation in alcohol after net treatment did not cause further shrinkage (only standard length measured).

To adjust the shrinkage models (Table 4) to predict live size from net-treated and Formalin-preserved size (equivalent to field-collected larvae), the preserved size is multiplied by 1.03. No adjustments are needed for alcohol-preserved samples.

The difference in shrinkage between laboratory-preserved larvae and net-treated and preserved larvae of the same initial live size decreased with age. For example, 3 mm larvae that were net treated and preserved in Formalin shrank 15% more in standard length than 3 mm larvae that were laboratory preserved in Formalin, but shrinkage of 20 mm larvae was the same for both treatments (Table 5). Shrinkage of laboratory-preserved larvae in Formalin probably decreases to something <8% (Table 5) as the skeleton develops and ossification occurs. Formalin preservation of 90 mm and larger salmon, *Oncorynchus* spp., smolts caused 3-4% shrinkage in length (Parker 1963). Laboratory shrinkage of northern anchovy after transformation may be similar; thus, shrinkage of net-collected and preserved northern anchovy >35 mm (Table 5) should be similar to shrinkage of laboratory-preserved fish >35 mm.

TABLE 5.—Comparison of standard length for live (L), laboratory-preserved and net-treated northern anchovy larvae (X_1). Numbers in parentheses are preserved length divided by live length (ratio of 1.00 = no shrinkage).

Live size (mm)	Estimated preserved size (mm)			
	Laboratory[1]		Net-treated[2]	
	Alcohol	Formalin	Alcohol	Formalin
3	3 (1.00)	2.76 (0.92)	2.38 (0.79)	2.31 (0.77)
5	5 (1.00)	4.59 (0.92)	4.10 (0.82)	3.98 (0.80)
10	10 (1.00)	9.18 (0.92)	8.77 (0.88)	8.51 (0.85)
15	15 (1.00)	13.78 (0.92)	13.81 (0.92)	13.40 (0.89)
20	20 (1.00)	18.37 (0.92)	18.99 (0.95)	18.42 (0.92)
25			24.21 (0.97)	23.48 (0.94)
30			29.40 (0.98)	28.52 (0.95)
35			34.56 (0.99)	33.52 (0.96)
40			39.68 (0.99)	38.49 (0.96)
45			44.77 (0.99)	43.43 (0.97)
50			49.84 (1.00)	48.34 (0.97)

[1]Includes 30 s handling time; no shrinkage in alcohol and 8% shrinkage in Formalin (see text).
[2]Estimated preserved size calculated from Equation (4) for 10 min net treatment; size adjusted for 3% additional shrinkage in Formalin (see text and Table 4).

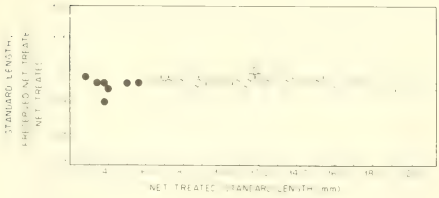


FIGURE 7.—Size specific shrinkage of northern anchovy larvae preserved in Formalin after 10-min net treatment. Dots are means of 10 larvae. Circles represent individual fish.

Eye Diameter

Netting live larvae for 10 min caused the eye diameter to shrink an average of 0.0443±0.0069 mm, and Formalin preservation after net treatment caused an increase in eye diameter that averaged 0.0177±0.0046 mm. The increase in eye diameter after preservation was similar to the increase after preservation noted for eye diameter of laboratory-preserved larvae. The t-tests for paired data (n=23) showed that in all cases the differ-

ences between treatments (live, net treated, and preserved) were significant ($P<0.01$). Even though these differences were significant, the small changes in eye diameter size caused by net treating and preserving probably are not important for calibration of size of field-collected larvae. Thus eye diameter should be a useful parameter for estimating average live standard length of field-collected larvae (Table 1).

DISCUSSION AND CONCLUSION

The causes of antemortem shrinkage of fish larvae are not completely understood. Before death, appearance of the body changes from translucent to opaque. This phenomenon is an indicator of ensuing death of larvae in rearing experiments. Autolysis, digestion of tissues by their own enzymes, is occurring during this antemortem period (Theilacker 1978), and the enzymatic action on proteins may cause denaturation, thus the color change and shrinkage. Shrinkage also may be caused by an osmoregulatory problem. An inability to osmoregulate may develop from loss of mucus by abrasion after contact with a surface. The internal osmolar concentration of another clupeoid larva, Pacific sardine, *Sardinops sagax*, is 0.24 M and that of seawater 0.56 M (Lasker and Theilacker 1962). If a larva were unable to osmoregulate, this difference in osmolarity would cause it to lose fluid and shrink.

The amount of shrinkage that occurred before larvae were killed in a preservative was dependent on larval fish size and the extent of "handling" (measuring and netting). The elapsed time of surface contact was the main determinant of final length. This was especially noticeable while measuring small, 3-7 mm larvae. As larvae increased in size and ossification progressed, net-treatment shrinkage decreased.

Preserving larvae after handling caused additional shrinkage that was a constant proportion of size. Laboratory-preserved shrinkage in Formalin included a 30 s handling time; shrinkage in Formalin was constant at 8% and independent of size. Preserving larvae that had been retained in a net caused an additional 3% shrinkage; the additional shrinkage was nearly a constant proportion of size.

Farris' (1963) results on shrinkage of laboratory-preserved, 3-6 mm yolk-sac Pacific sardine larvae agree with my results. He found Formalin shrinkage of standard length ranged between 7 and 11%, similar to the 8% shrinkage for laboratory-preserved northern anchovy in my study. Rosenthal et al. (1978) reported a 16% shrinkage of newly hatched, 2 mm larvae of the sea bream, *Chrysophrys major*. The larvae were anesthesized with MS-222 and measured with a projector prior to preservation in Formalin. It appears that handling of the sea bream was minimal; however, MS-222 has been reported to interfere with osmoregulation (Parker 1963), and an inability to osmoregulate would cause a greater shrinkage. Blaxter (1971) reported on a net-shrinkage experiment that was similar to my study. After his net treatment, mean live size of 22 herring larvae (10.77 mm) decreased by 17%; Formalin fixation caused an additional 3-5% shrinkage for a total of 20-22%. He noted the larvae were dead after netting, but the elapsed time is unknown. In this study, the netted 11 mm northern anchovy were usually dead after 20 min, and the total shrinkage of the 20-min treated 11 mm northern anchovy was about 18%, similar to Blaxter's experiment.

If the larvae to be measured are badly damaged or partially digested, the models generated in this study, which describe live body proportions and shrinkage, could be used to estimate average fish length from size of head or eye. Packard and Wainwright (1974) found that eye diameter of young herring (up to 100 mm) was a useful reference parameter for estimating both size and weight. Because eye diameter of northern anchovy changed little during netting and preservation, eye diameter may be a useful parameter for estimating average live size of field-collected larvae. However, use of eye diameter to estimate live standard length assumes that the relation between eye diameter and standard length is the same for laboratory-reared and field-collected larvae. Balbontin et al. (1973) and Blaxter (1976) have shown that morphological differences exist between reared and wild fish of the same length, thus the assumption, that the body forms of reared and wild northern anchovy larvae are similar, may be invalid. However, as I have shown in this study, the method of handling larvae prior to preservation causes shrinkage differences that could be interpreted as morphological differences.

The most important use of the shrinkage models is to predict live size, and thus age, of sea-collected northern anchovy larvae so that results from laboratory larval fish studies can be related to the sea. Use of the standard length shrinkage model (Table 4) should give the best estimate of live size

for field collected larvae. The standard length model can probably be applied to shrinkage of all clupeidlike larvae if the patterns of calcification are similar.

FORTRAN computer programs for the nonlinear models are available at the Southwest Fisheries Center La Jolla Laboratory.

ACKNOWLEDGMENTS

I especially wish to thank James Zweifel for his consultation, encouragement, and assistance in developing these models. Thanks also to Joe Caruso for his interest in the study and patient assistance with the computer programs, Jack Metoyer for assisting with the tedious task of measuring larvae, Kathleen Coleman for helping me by typing the draft and the tables, and Lorraine Prescott for typing the final draft. John Hunter, Reuben Lasker, and two anonymous reviewers read the manuscript and offered many helpful suggestions.

LITERATURE CITED

AHLSTROM, E. H.
1976. Maintenance of quality in fish eggs and larvae collected during plankton hauls. *In* H. F. Steedman (editor), Zooplankton fixation and preservation, p. 313-318. Monogr. Oceanogr. Methodol. 4.

BALBONTIN, F., S. S. DESILVA, AND K. F. EHRLICH.
1973. A comparative study of anatomical and chemical characteristics of reared and wild herring. Aquaculture 2:217-240.

BLAXTER, J. H. S.
1971. Feeding and condition of Clyde herring larvae. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 160:128-136.
1976. Reared and wild fish—how do they compare? Proc. 10th Eur. Symp. Mar. Biol. 1:11-26.

CONWAY, G. R., N. R. GLASS, AND J. C. WILCOX.
1970. Fitting nonlinear models to biological data by Marquardt's algorithm. Ecology 51:503-507.

FARRIS, D. A.
1963. Shrinkage of sardine (*Sardinops caerulae*) larvae upon preservation in buffered formalin. Copeia 1963:185-186.

HUNTER, J. R.
1976. Culture and growth of northern anchovy, *Engraulis mordax*, larvae. Fish. Bull., U.S. 74:81-88.

LASKER, R., H. M. FEDER, G. H. THEILACKER, AND R. C. MAY.
1970. Feeding, growth and survival of *Engraulis mordax* larvae reared in the laboratory. Mar. Biol. (Berl.) 5:345-353.

LASKER, R., AND G. H. THEILACKER.
1962. Oxygen consumption and osmoregulation by single Pacific sardine eggs and larvae, (*Sardinops caerulea* Girard). J. Cons. 27:25-33.

LEONG, R.
1971. Induced spawning of the northern anchovy, *Engraulis mordax* Girard. Fish. Bull., U.S. 69:357-360.

METHOT, R. D., JR., AND D. KRAMER.
1979. Growth of northern anchovy, *Engraulis mordax*, larvae in the sea. Fish. Bull., U.S. 77:413-423.

PACKARD, A., AND A. W. WAINWRIGHT.
1974. Brain growth of young herring and trout. *In* J. H. S. Blaxter (editor), The early life history of fish, p. 499-507. Springer-Verlag, N.Y.

PARKER, R. R.
1963. Effects of formalin on length and weight of fishes. J. Fish. Res. Board Can. 20:1441-1455.

ROSENTHAL, H., D. KUHLMANN, AND O. FUKUHARA.
1978. Shrinkage of newly hatched larvae of the red sea bream (*Chrysophrys major* Temminck and Schlegel) preserved in Formalin. Arch. Fischereiwiss. 29:59-63.

RYLAND, J. S.
1966. Observations on the development of larvae of the plaice, *Pleuronectes platessa* L., in aquaria. J. Cons. 30:177-195.

SMITH, P. E., AND S. L. RICHARDSON.
1977. Standard techniques for pelagic fish egg and larva surveys. FAO Fish. Tech. Pap. 197,

THEILACKER, G. H.
1978. Effect of starvation on the histological and morphological characteristics of jack mackerel, *Trachurus symmetricus*, larvae. Fish. Bull., U.S. 76:403-414.

THEILACKER, G. H., AND M. F. MCMASTER.
1971. Mass culture of the rotifer *Brachionus plicatilis* and its evaluation as a food for larval anchovies. Mar. Biol. (Berl.) 10:183-188.

ASPECTS OF LARVAL ECOLOGY OF *SQUILLA EMPUSA* (CRUSTACEA, STOMATOPODA) IN CHESAPEAKE BAY

STEVEN G. MORGAN[1]

ABSTRACT

Larvae of *Squilla empusa* were collected from the plankton and were laboratory-reared in 16 combinations of temperature and salinity to determine their tolerances. Larvae survived longer and molted more frequently when reared at 25‰ and 20° or 25° C, which corresponds to the natural conditions of Chesapeake Bay when the larvae were collected.

A 2-yr planktonic survey conducted in the lower region of the bay by the Virginia Institute of Marine Sciences was compared with a survey made at the bay mouth in 1976. The seasonal occurrence of *Squilla empusa* larvae extended from the last week of July until the first week of October with a peak abundance occurring about the first week of September. The peak abundance in the lower region of the bay was 0.37 larva/m^3 in 1971 and 0.59 larva/m^3 in 1972. Four of the nine stages were not captured. Collections taken at the bay mouth in 1976 with a ½ m net captured all stages and the peak abundance was determined to be 0.27 larva/m^3. The larvae were more abundant in the higher salinity waters of the channel areas and eastern portion of lower Chesapeake Bay. A large-mouth plankton net with relatively coarse mesh should be towed at night to ensure the collection of all larval stages since the larger larvae are apparently able to avoid small nets.

The Order Stomatopoda is a small group of primitive, specialized crustaceans which reside primarily in shallow tropical marine waters. Of the 350 species (Caldwell and Dingle 1976) only a few extend into temperate waters, *Squilla empusa* among them. This mantis shrimp, which attains a length of 20 cm, is found from Massachusetts to northern South America and is quite abundant throughout its range, including Chesapeake Bay (Brooks 1878; Cowles 1930; Wass 1972).

Stomatopod larvae are often found in great swarms, particularly in tropical waters where adults are most abundant. The planktonic larval stages compose a substantial portion of the neritic plankton and constitute a considerable part of the diet of reef fishes, jacks, scads, herrings, snappers, and commercially important pelagic fishes such as tunas and mackerel (Sunier 1917; Fish 1925; Reintjes and King 1953; Randall 1967; Dragovich 1970).

Squilla empusa larvae are large crustacean larvae, attaining 17.5 mm long. The larvae undergo nine pelagic stages before settling to the bottom as postlarvae (Morgan and Provenzano 1979). Brooks (1878) found stomatopod larvae he assumed were those of *S. empusa* present in Chesapeake Bay from early July to the middle of August in the greatest abundance, but he discontinued the study before the larvae had completed their metamorphosis. No other data on larvae of this species have been added to the literature since.

Due to the paucity of ecological information on the larvae of this prevalent crustacean, an investigation was undertaken to determine their seasonal occurrence, distribution, and abundance in Chesapeake Bay. The abundance and duration of the larvae as part of the plankton may be important factors in the ecology of the bay, since the larvae not only serve as food for a variety of organisms, including commercially important fishes, but are also rapacious predators themselves, thriving on other members of the planktonic community.

In recent years the effects of temperature and salinity on the larval development of decapod crustaceans have been studied, but no studies have been made on the temperature and salinity tolerance for the larvae of any species within the Order Stomatopoda. Temperature and salinity are critical factors affecting the survival of marine and estuarine organisms, especially during the sensitive developmental stages upon which the success of the species relies. Thus, a qualitative determination of the temperature and salinity tol-

[1]Institute of Oceanography, Old Dominion University, Norfolk, Va.; present address: Duke University Marine Laboratory, Pivers Island, Beaufort, NC 28516.

Manuscript accepted February 1980.
FISHERY BULLETIN: VOL. 78, NO. 3, 1980.

erance of *S. empusa* is presented and a comparison of the laboratory result with the observed distributions is made.

METHODS

Research Applied to National Needs (RANN) Survey

The sampling area extended from lat. 37°40′ N, just north of the Rappahannock River, to the bay mouth, an area covering 1,300 km of the lower Chesapeake Bay (Figure 1). The survey area was divided into eight subareas designated A through H. A, D, and G were situated in the western portion and B, F, and H in the eastern section of the bay. These divisions were based on salinity differences in the bay, while areas C and E were separated because they represented channel areas.

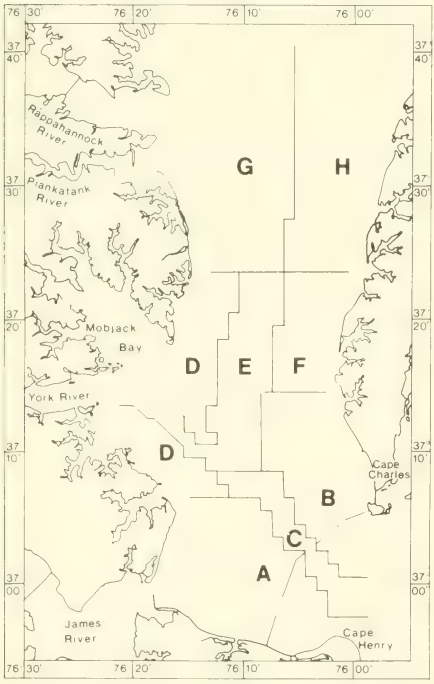


FIGURE 1.—Subareas (A-H) of RANN survey, August 1971 to July 1973, in lower Chesapeake Bay, Va.

The study area, consisting of 688 stations set 1.8 km apart, was sampled from August 1971 to July 1973. Three to five stations were randomly selected from each subarea to be sampled each month.

The plankton samples collected during the RANN survey were taken with a bongo sampler, having a mouth diameter of 18.7 cm (8 in) and equipped with 202 μm mesh nets. Stepped oblique tows were taken for varying lengths of time at each station, depending on station depth. A submersible pump was used at depth intervals of 2 m to gather hydrographic data. The temperature and salinities taken at each interval from each station were then averaged. All tows were taken during daylight. The stomatopod larvae were sorted from the general catch by the Virginia Institute of Marine Science staff and staged by the author.

Cape Henry Survey

Using the Old Dominion University RV *Linwood Holton*, larval specimens of *S. empusa* were collected weekly at Cape Henry where a population of adults exists. By using a ½ m plankton net (153 μm mesh), 10 min stepped oblique tows were accomplished as the ship circled the collection site at idle speed. The volume of water filtered through the net was calculated from the duration of the tow and the area of the net because the flowmeters employed yielded wildly erratic readings. The volume of water filtered for a 10-min tow was calculated to be 47.6 m^3. Surface and bottom water temperatures and salinities were recorded for each tow, using an inductive salinometer with a 45.7 m cable.

Upon collection each plankton sample was placed in a 1.9 l (½-gal) jar and filled with seawater. Samples containing large amounts of biomass were split into two such jars to facilitate the survival of the stomatopod larvae until they could be separated from the sample. As many larvae as possible were extracted from the samples aboard the ship and the task was completed in the laboratory. These larvae were placed in 1.9 l jars filled with seawater and were grouped according to size so that cannibalism would be minimal. The jars were aerated until the samples reached the laboratory, whereupon the larvae were placed in compartmentalized plastic trays, one per compartment. Each compartment measured 4.5 × 5 × 4 cm. Medium used for rearing the larvae was

made from Instant Ocean Synthetic Sea Salts[2] (Aquarium Systems, Inc., Eastlake, Ohio) and tapwater.

Larvae representing all nine developmental stages of *S. empusa* were reared in 16 combinations of temperature and salinity, each having a similar composition of larval stages. The experimental temperatures used were 10°, 15°, 20°, and 25° C, and salinities were 10, 15, 25, and 35‰, chosen because they represent the range of conditions the larvae might be expected to encounter in the lower Chesapeake Bay. The salinities of 20 and 30‰ were omitted from the experimental regime because insufficient numbers of larvae were obtained to determine their tolerances to all intermediate salinities as well as to the more extreme salinities. Thirty-six larvae were subjected to each temperature-salinity combination. Because the larvae were not hatched in the laboratory under the temperature-salinity combination at which they would be reared, some larvae were subjected to changes as great as 5° C and 10‰ per day until the experimental value was attained. No light cycle was used in the experiment, the larvae being maintained in total darkness except for 10-min periods when the larvae were given fresh food and water.

Each larva was reared in 25 ml of water and given freshwater and approximately 30 *Artemia salina* nauplii/ml daily. Great increases in size from the first to the last stage necessitated adjustments in food size and quantity. At about the fifth stage of development food was switched from *A. salina* nauplii to decapod zoeae or *A. salina* larvae grown on a yeast or algal culture. While changing the culture medium, observations were recorded on the progress of each larva regarding the frequency of molting, duration of larval development, survival, and the stage of development.

Percent survival and molting frequency are often used as measures of success of larvae under different temperature-salinity regimes, but were not meaningful in this experiment because the larvae were captured at different stages of development and different places in the molt cycle. Therefore, the length of survival and number of molts were used as the standards of success. The temperature and salinity combinations which promoted the greatest number of molts and the longest periods of survival among the larvae were considered to be most conducive to the larval development of *S. empusa*, because the larvae were not only surviving best but were also maturing fastest. The mean number of ecdyses and days of survival were calculated for each larva and then collective means were figured for each temperature-salinity combination. In this way a general indication of success of populations under varying temperature and salinity conditions could be determined.

RESULTS

Seasonal Occurrence

The RANN survey extended from 16 August 1971 until 25 July 1973, and *S. empusa* larvae were found in the Chesapeake Bay only from late July to mid-September or late October (Figure 2). During these months in 1971 the RANN study sampled on 16-19 August, 21-23 September, and 26-29 October, while in 1972 samples were taken on 24-27 July, 15, 17, 18, 21 August, 12-14 September, and 16, 18, 24 October. In 1973, sampling was conducted on 23-25 July.

The monthly sampling program used by the RANN program left the larval occurrence of *S. empusa* somewhat unclear. In both years of the survey, larvae were found on the first day of sampling in July, 24 July 1972 and 23 July 1973; since a month elapsed between the June and July samplings, however, the earliest appearance of the

FIGURE 2.—Larval abundance of *Squilla empusa* collected from the lower Chesapeake Bay from August 1971 to July 1973 and from June to November 1976.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

larvae could have gone undetected. The same problem occurred in defining the time of disappearance, for larvae were abundant on 14 September 1971 and 1972 but the next sampling was not conducted until 26 October 1971 and 16 October 1972. Only one Stage I larva was found in October 1971.

The Cape Henry data helped to determine more closely the planktonic duration of the larvae since a weekly sampling program was followed when weather permitted. In agreement with the RANN survey, the first larvae appeared in late July. Larvae were present on 28 July but none were found on 20 July. Larvae were found until 6 October; none were collected on 13 October. From the RANN and Cape Henry surveys it is apparent that the planktonic occurrence of *S. empusa* extends from the last week of July until the first week of October, a period of almost 11 wk or about 2½ mo.

Only Stages I-IV and IX were collected by the RANN survey (Figure 3). Bearing this in mind, the RANN data showed the month of maximum abundance to be August, with 0.37 larva/m^3 collected in 1971 and 0.59 larva/m^3 in 1972; September, July, and October trailed in order of decreasing abundance (Figure 2). The Cape Henry data, on the other hand, showed a peak abundance in September with 0.27 larva/m^3 in 1976 followed by August, July, and October.

All nine stages were collected during the Cape Henry sampling program (Figure 4). In July, when the larvae first began to appear, Stages I and II were the only stages collected in abundance and they were more numerous than in any following month. Several specimens of Stages V and VIII were also captured. All larval stages were present in August with younger larvae generally being predominant over older larvae. By early September the larvae had reached their peak abundance. Although some of the younger larval stages had begun to decline, they were still predominant. The latest larval stages, VIII and IX, were becoming increasingly abundant until October when only Stage IX larvae were obtained.

The abundance of larvae caught from each subarea during the RANN survey indicates that larvae were more prevalent in the eastern and channel areas of the bay than in the western portion

FIGURE 3.—Abundance of larval stages (I-IX) of *Squilla empusa* collected from the lower Chesapeake Bay from August 1971 to July 1973. Larval stages described in Morgan and Provenzano (1979).

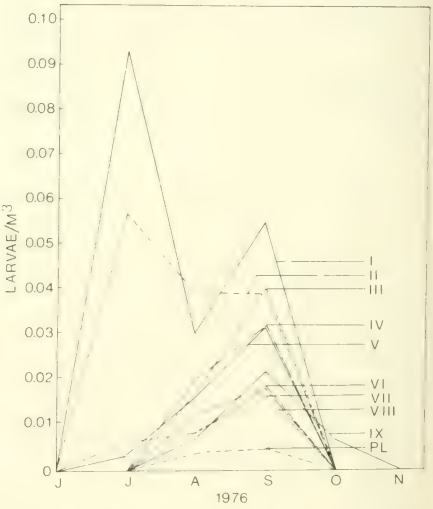


FIGURE 4.—Abundance of larval stages (I-IX) and postlarva (PL) of *Squilla empusa* collected at Cape Henry, lower Chesapeake Bay, from June to October 1976. Larval stages described in Morgan and Provenzano (1979).

TABLE 1.—Larval abundance of *Squilla empusa* with mean temperatures and salinities for each subarea (Figure 1) of the lower Chesapeake Bay for August and September 1971 and 1972.

	Lower			Middle			Upper	
	West A	Channel B	East C	West D	Channel E	East F	West G	East H
1971:								
Larvae/m³	0.13	0.36	0.19	0.12	0.28	0.28	0.05	0.47
Mean salinity	24.8	25.5	26.0	20.1	22.4	22.9	17.7	20.8
Mean temperature, °C	24.5	24.3	23.7	25.5	25.1	24.4	24.9	24.7
1972:								
Larvae/m³	0.43	0.44	0.41	0.04	0.70	0.89	0.02	0.08
Mean salinity	20.5	21.0	23.0	17.3	19.4	19.4	15.3	15.8
Mean temperature, °C	23.4	23.4	23.1	24.3	23.9	23.5	24.2	23.9
1971 and 1972:								
Larvae/m³	0.30	0.40	0.33	0.08	0.49	0.75	0.03	0.28
Mean salinity	22.7	23.2	24.5	18.7	20.9	21.1	16.5	18.3
Mean temperature, °C	23.9	23.9	23.4	24.9	24.5	24.0	24.6	24.3

(Table 1). Larvae were also more abundant in the lower regions of the sampling area than in the upper (subareas G and H).

Squilla empusa larvae occur in the Chesapeake Bay when the mean temperatures are the highest of the year. The first larvae were encountered in July for both 1972 and 1973 when mean temperatures were 25.2° and 24.5° C. The larvae were most abundant in August when the mean temperatures were 24.9° and 24.2° C in 1971 and 1972. The mean temperatures declined in September along with the abundance of larvae until larvae were rarely found or not found in October when temperatures were 19.7° and 19.4° C in 1971 and 1972. The mean salinity during the seasonal occurrence of the larvae in 1971 and 1973 fluctuated between 21.5 and 23.1‰, while in 1972 it was much lower as a result of Tropical Storm Agnes. In July 1972 the mean salinity was 16.5‰ and it increased to 21.2‰ in October when larvae no longer occurred in the plankton.

Temperature and Salinity Tolerance

Although none of the 576 larvae reared at the 16 different temperature and salinity combinations was reared through the entire pelagic development to metamorphosis, larvae survived well and molted frequently at 2 of the test combinations. At 20° C-25‰ and 25° C-25‰, 47% of the larvae molted three or more times, 24% underwent at least five ecdyses, and 3% molted seven times over a 6-wk period. Metamorphosis to postlarva occurred 34 times and was not a problem in the rearing process.

In general, larvae fared best at higher temperatures and salinities (20°, 25° C, 25, 35‰) and were least successful at the lower temperatures and salinities (10°, 15° C, 10, 15‰). Excluding larvae reared at 10° C, the longest survival and greatest number of molts occurred at salinities of 25‰ followed by 35, 15, and 10‰ in order of decreasing length of survival and number of molts (Figures 5, 6). Length of survival at 25°, 20°, and 15° C was similar but at 25° and 20° C the mean number of molts was much higher. At 10° C larvae

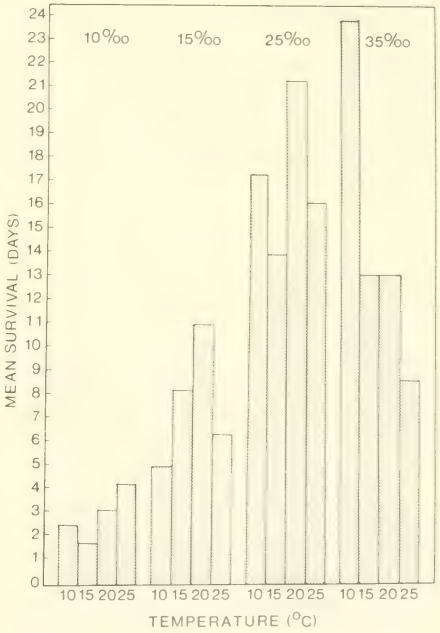


FIGURE 5.—Average survival, in days, for all larval stages of *Squilla empusa*, grouped by 16 temperature-salinity combinations according to salinity.

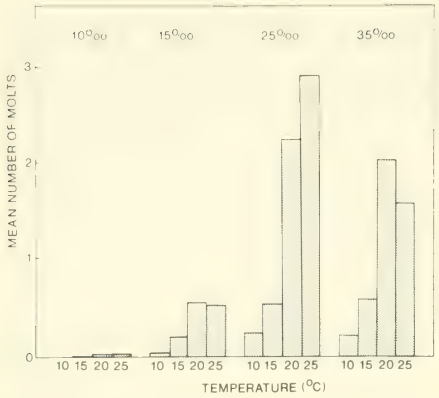


FIGURE 6.—Average number of ecdyses for all larval stages of *Squilla empusa* grouped by 16 temperature-salinity combinations according to salinity.

molted rarely and did not survive long at the lower salinities. At higher salinities molting occurred slightly more often and larvae at 10° C-35‰ were able to endure the longest of any of the combinations. Some of these larvae persisted for as long as 47 d, but usually without molting. Since these larvae did not appear to feed and moved only slightly, the low temperature only seemed to delay their deaths.

DISCUSSION

The information provided by the RANN survey only loosely delimited the seasonal occurrence of *S. empusa* larvae in Chesapeake Bay because of infrequent sampling. A weekly sampling program would have been beyond the scope of the investigation considering that the purpose of the RANN study was to survey the entire zooplankton community of the lower Chesapeake Bay over a 2-yr period. Supplemental data taken at Cape Henry combined with the RANN data indicate that the seasonal occurrence of *S. empusa* larvae extends from late July to early October, a period of about 11 wk. Observations made by Brooks (1878) concerning the planktonic duration of *S. empusa* larvae are in agreement with the current study, but the time of occurrence was slightly earlier in the previous study. Larvae were present in the plankton from early July through August when Brooks discontinued the study. Eleven weeks is a fairly short planktonic duration for stomatopod larvae. The temperate species *Oratosquilla oratoria*, common in Japan, has a 5-mo duration (Senta 1967), and *Pterygosquilla armata schizodontia* was discovered to remain in the plankton for up to 9 mo (Pyne 1972).

Although Brooks (1878) found the *S. empusa* larvae in great abundance, sometimes collecting 200 or 300 in a single evening from the mouth of the James River, both the RANN data and the Cape Henry data showed that the larvae were never abundant. Because only five of the nine larval stages were collected during the RANN survey the abundance values are inordinately low. Apparently, the larger larvae are able to avoid the small bongo plankton nets. Great quantities of Stage I larvae were captured throughout the larval season but far fewer numbers of Stage II were caught and fewer still Stage III larvae were caught and so on until Stages V-VIII were not collected at all. The large decreases seem to be too great to be accounted for by mortality alone.

It is possible that the large, quick-moving (pers. obs.) stomatopod larvae could avoid the small mouth of the net which was easily detectable since sampling was conducted during daylight (Fleminger and Clutter 1965; McGowan and Fraundorf 1966; Murphy and Clutter 1972). Olney (1978) also used data collected during the RANN survey and found evidence of avoidance in other large, agile zooplankters, particularly mysids and fish larvae. A ½ m net and night sampling were used during the Cape Henry survey and the elusive stages missed by the bongo sampler were captured. Although all nine stages were collected, peak abundance was still slightly lower than the RANN values. The lower value may have resulted from the use of a smaller mesh net, from not employing a flowmeter to obtain better filtration estimates, or from yearly fluctuations in the population; but, the abundance figures determined by the RANN and Cape Henry surveys are low for an organism that has been considered to be abundant in Chesapeake Bay (Brooks 1878; Cowles 1930; Wass 1972).

The RANN data showed the month of maximum abundance to be August, but the Cape Henry data demonstrated a peak abundance in early September. Again, this discrepancy may be attributed to normal yearly variation, but it probably resulted from the RANN program having sampled only the younger element of the population.

Larvae reared in the laboratory survived longest and molted the greatest number of times at 20° C-25‰ and 25° C-25‰ which corresponds to the temperatures and salinities found in the bay where the larvae were most abundant. The mean temperature of the bay from July through September, the season of larval occurrence of *S. empusa*, ranged from 19.7 ° to 25.2° C while the mean salinity was recorded from 21.5 to 23.1‰ in 1971 and 1973.

The greater abundance of larvae in the eastern and channel subareas of the bay is likely a result of the higher salinities. In Chesapeake Bay salinities are higher on the eastern side than on the western side due to the earth's rotation (Coriolis force) and the differences are enhanced by the larger inflow of freshwater from rivers on the western side (Pritchard 1952). The lower salinities of the upper reaches of the sampling area are also probably responsible for the lesser larval abundances in subareas G and H.

In 1972, Tropical Storm Agnes produced the most extensive flooding and greatest freshwater runoff in Chesapeake Bay in many decades, if not centuries, causing the distribution and abundance of most estuarine organisms to be seriously disrupted (Andrews 1973). The mean salinity of the lower Chesapeake was reduced to 16.5‰ in July only to increase to 19.4‰ in October. Although the larvae were more abundant in 1972 than in 1971, the reduced salinity resulted in a distribution compressed into the more southern subareas where the salinity was greater. Few larvae were captured in subareas D, G, and H where salinities ranged from 15.3 to 17.3‰, which would be expected considering the poor development of larvae reared at 15‰ during the temperature and salinity experiment. Grant et al. (1976) found other zooplankters in the lower Chesapeake Bay to be as abundant in 1972 as in 1971 and their distributions were also compressed in 1972.

Of the *S. empusa* larvae reared at the most favorable temperature and salinity combinations for survival and growth, 3% of the larvae were reared through eight of the nine larval stages in 6 wk, indicating that the length of the pelagic larval development would be slightly longer than 6 wk. However, the appearance of the postlarvae in the bay 1 mo after the initial appearance of the larvae indicates a substantially briefer period of larval development, provided that all larvae originated within the bay. The development of the larvae reared in the laboratory may have been extended as a result of dietary insufficiencies and an overall more stressful environment. Furthermore, the few specimens of stages V and VIII collected early in the 1976 larval season may have drifted into the bay from more southerly populations where eggs may have hatched earlier and been transported by currents into Chesapeake Bay. Nevertheless, since all larval stages and the postlarva were collected in Chesapeake Bay throughout their seasonal occurrence, it appears that the populations of *S. empusa* in the bay is self-sustaining. In addition, the temperature and salinity tolerances of the larvae correspond to those of the adults, which may occur in salinities as low as 16‰, but are most abundant in waters >25‰ (Cowles 1930; Gunter 1950; Parker 1956; Lee and McFarland 1962).

ACKNOWLEDGMENTS

I am indebted to George C. Grant of the Virginia Institute of Marine Science who made available plankton samples collected during the RANN survey of the lower Chesapeake Bay. He also kindly provided the map of the survey area and commented on the manuscript.

Thanks are also due Anthony J. Provenzano, Jr. for his guidance during the investigation and his comments on the manuscript.

This work was supported in part by the National Science Foundation Grant DEB-76-11716.

LITERATURE CITED

ANDREWS, J. D.
1973. Effects of Tropical Storm Agnes on epifaunal invertebrates in Virginia estuaries. Chesapeake Sci. 14:223-234.

BROOKS, W. K.
1878. The larval stages of *Squilla empusa* Say. Johns Hopkins Univ., Chesapeake Zool. Lab. Sci. Res. 1878:143-170.

CALDWELL, R. L., AND H. DINGLE.
1976. Stomatopods. Sci. Am. 234(1):80-89.

COWLES, R. P.
1930. A biological study of the offshore waters of Chesapeake Bay. Bull. U.S. Bur. Fish. 46:276-381.

DRAGOVICH, A.
1970. The food of skipjack and yellowfin tunas in the Atlantic Ocean. U.S. Fish Wildl. Serv., Fish. Bull. 68:445-460.

FISH, C. J.
1925. Seasonal distribution of the plankton of the Woods Hole region. Bull. U.S. Bur. Fish. 41:91-179.

FLEMINGER, A., AND R. I. CLUTTER.
1965. Avoidance of towed nets by zooplankton. Limnol. Oceanogr. 10:96-104.

GRANT, G. C., B. B. BRYAN, F. JACOBS, AND J. E. OLNEY.
1976. Effects of Tropical Storm Agnes on zooplankton in

the lower Chesapeake Bay. *In* The effects of Tropical Storm Agnes on the Chesapeake Bay Estuarine System, p. 425-442. Chesapeake Research Consortium, Inc. CRC Publ. 54.

GUNTER, G.
1950. Seasonal population changes and distributions as related to salinity, of certain invertebrates of the Texas coast, including the commercial shrimp. Publ. Inst. Mar. Sci., Univ. Tex. 1(2):7-51.

LEE, B. D., AND W. N. MCFARLAND.
1962. Osmotic and ionic concentrations in the mantis shrimp *Squilla empusa* Say. Publ. Inst. Mar. Sci., Univ. Tex. 8:126-142.

MCGOWAN, J. A., AND V. J. FRAUNDORF.
1966. The relationships between size of net used and estimates of zooplankton diversity. Limnol. Oceanogr. 11:456-469.

MORGAN, S. G., AND A. J. PROVENZANO, JR.
1979. Development of pelagic larvae and postlarva of *Squilla empusa* (Crustacea, Stomatopoda). Fish. Bull., U.S. 77:61-90.

MURPHY, G. I., AND R. I. CLUTTER.
1972. Sampling anchovy larvae with a plankton purse seine. Fish. Bull., U.S. 70:789-798.

OLNEY, J. E.
1978. Planktonic fish eggs and larvae of the lower Chesapeake Bay. M.A. Thesis, Coll. William and Mary, Williamsburg, Va., 123 p.

PARKER, R. H.
1956. Macro-invertebrate assemblages as indicators of sedimentary environments in East Mississippi Delta region. Am. Assoc. Pet. Geol. Bull. 40:295-376.

PRITCHARD, D. W.
1952. Salinity distribution and circulation in the Chesapeake Bay estuarine system. J. Mar. Res. 11:106-123.

PYNE, R. R.
1972. Larval development and behaviour of the mantis shrimp *Squilla armata* Milne Edwards (Crustacea: Stomatopoda). J. R. Soc. N.Z. 2:121-146.

RANDALL, J. E.
1967. Food habits of reef fishes of the West Indies. Stud. Trop. Oceanogr. (Miami) 5:665-847.

REINTJES, J. W., AND J. E. KING.
1953. Food of yellowfin tuna in the central Pacific. U.S. Fish Wildl. Serv., Fish. Bull. 54:91-110.

SENTA, T.
1967. Seasonal abundance and diurnal migration of alima larvae of *Squilla oratoria* in the Seto Inland Sea. [In Jpn., Engl. summ.] Bull. Jpn. Soc. Sci. Fish. 33:508-512.

SUNIER, A.
1917. The Stomatopoda of the collection "Visscherij-station" at Batavia. Contrib. Faune Indes Neerl. 1(4):62-75.

WASS, M. L. (compiler).
1972. A check list of the biota of lower Chesapeake Bay. Va. Inst. Mar. Sci., Spec. Sci. Rep. 65, 290 p.

EGG AND LARVAL DEVELOPMENT OF THE SPOT, *LEIOSTOMUS XANTHURUS* (SCIAENIDAE)[1]

ALLYN B. POWELL AND HERBERT R. GORDY[2]

ABSTRACT

The egg and larval development of the spot, *Leiostomus xanthurus*, was described mainly from laboratory-reared specimens. Egg diameters averaged 0.80 mm and ranged from 0.72 to 0.87 mm. The number of oil globules varied, but coalesced during development. Oil globule diameters of eggs with one globule averaged 0.21 mm and ranged from 0.18 to 0.28 mm. Newly hatched larvae measured 1.6-1.7 mm standard length, had a single oil globule located at the posterior margin of the yolk sac, and were inconspicuously pigmented. Late yolk-sac larvae developed a characteristic pigment pattern of a single row of melanophores along the ventral midline that persisted throughout the larval period. An important pigment pattern—embedded pigment at the anterior of the gut—was first observed in clear and stained late flexion larvae (2.9 mm standard length). Vertebrae and anal fin pterygiophore counts were considered useful in separating spot from other sciaenids. Vertebral counts (25) were established by 4.6 mm standard length, and precaudal (10) and caudal (15) vertebrae were recognized at 5.1 mm standard length. Anal fin pterygiophores which numbered two fewer than the number of anal fin elements were established at 6.3 mm standard length.

The spot, *Leiostomus xanthurus* (Lacépède), is a commercially important sciaenid found along the Northwest Atlantic and Gulf of Mexico coasts from Massachusetts Bay to the Bay of Campeche (Johnson 1978). Spot spawns in offshore waters during late fall and early winter, throughout its range (Hildebrand and Cable 1930; Nelson 1969). The larvae are transported towards shore and into estuaries which serve as nursery areas (Fahay 1975; Chao and Musick 1977).

The eggs and yolk-sac larvae of spot have not been described. Pearson (1929) briefly described larvae ranging from 7 to 15 mm. Hildebrand and Cable (1930) described larvae in greater detail and attempted to distinguish spot larvae from morphologically similar larvae of Atlantic croaker, *Micropogonias undulatus* (the generic name change from *Micropogon* follows Chao 1978). Hildebrand and Cable (1934) summarized early life history data for 13 species of sciaenids, including spot, but the keys they prepared were limited since the early developmental stages for many species were unknown. Lippson and Moran (1974) and Johnson (1978) summarized early life history studies on sciaenids and included previously unpublished illustrations useful in separating spot and croaker larvae. Fruge and Truesdale (1978) and Powles and Stender (1978) described developmental stages of spot larvae from the Gulf of Mexico and the South Atlantic Bight. Fruge and Truesdale provided comparative data useful for separating larvae of spot from larvae of Atlantic croaker, while Powles and Stender emphasized characters useful in separating early sciaenid larvae.

In this paper we describe the life history of spot from egg to juvenile, using the dynamic approach of Ahlstrom and Ball (1954). Our objective is to provide descriptive information useful in identification and classification, as patterns of larval development and larval anatomical features may provide keys to possible relations among groups (Aprieto 1974). Furthermore, studies of variations of these patterns and features could provide keys to how environmental factors may affect larval development.

METHODS

Spot used for spawning were collected from a commercial long-haul seine in Back Sound off Harkers Island, N.C., during their spawning migration to the ocean. Eggs were obtained from fish using an induced spawning technique developed

[1]Contribution No. 80-27B of the Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOAA.

[2]Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOAA, Beaufort, NC 28516.

Manuscript accepted February 1980.
FISHERY BULLETIN: VOL. 78, NO. 3, 1980.

by Hettler et al.[3] This technique allows for a voluntary release of ova by females injected with human chorionic gonadotropin (HCG) and sperm by uninjected males. The quality of eggs produced by this technique is far superior to injecting HCG and manually removing and mixing gametes. The rotifer *Brachionus plicatilis*, cultured in the laboratory, was used as food for spot larvae till they were approximately 30 d old. Zooplankton captured from the field and predominated by copepod nauplii and copepodites were sporadically included in their diets during this period. Newly hatched *Artemia* nauplii were used as food for larvae older than about 30 d. Eggs and larvae were maintained at temperatures and salinities of ca. 20° C and ca. 30-35‰. Some advanced larvae and juveniles were collected with a modified neuston net (Hettler 1979) near Beaufort, N.C.

Two developmental series of larvae were used. Specimens in the first series were used for compiling morphometric data, describing pigment patterns and illustrating larval stages. Those in the second series were cleared with trypsin, stained with a combination of alcian blue and alizarin red according to Dingerkus and Uhler (1977), and Taylor and Van Dyke[4] and used for meristic studies. Egg stages follow those described by Ahlstrom and Ball (1954). The embryonic period was divided into three stages: early (fertilization to blastopore closure), middle (from blastopore closure until the tail twists out of the plane of the embryonic axis), and late (from tail twisting to hatching). Larval stages followed those described by Ahlstrom et al. (1976). The larval period was separated into the preflexion, flexion, and postflexion stages associated with the development of the caudal fin; the stages occurring before, during, and after the upward flexion of the notochord tip. We also included a yolk-sac stage, which we believed should be treated separately.

Pterygiophore nomenclature followed Houde and Potthoff (1976). Nominal, full complement counts were taken from Johnson (1978), although we obtained pectoral ray counts directly from 15 specimens (University of North Carolina; UNC 563). Measurements from eggs and larvae preserved in 5% buffered Formalin[5] are identified as follows:

Standard length (SL) — in preflexion and flexion larvae, the horizontal distance from the tip of the snout to the tip of the notochord. In postflexion larvae, from the tip of the snout to the base of the hypural plate.

Preanus length — horizontal distance from the tip of the snout to the posterior part of the anus.

Head length — horizontal distance from the tip of the snout to the posterior margin of the otic capsules in yolk-sac larvae and the horizontal distance from the tip of the snout to the opercular margin in other larvae and juveniles.

Snout length — horizontal distance from the tip of the snout to the anterior margin of the pigmented region of the eye.

Eye diameter — maximum horizontal width of the pigmented eye.

Body depth — the vertical depth of the body measured at the pectoral fin base exclusive of the finfold.

RESULTS

Embryonic Development

General

Spot eggs are pelagic. The chorion was transparent and unsculptured. The yolk was unsegmented, unpigmented, and the perivitelline space narrow in live eggs. Oil globules were yellow. We have obtained batches of eggs with almost all single oil globules, almost all multiple oil globules, or a gradient between these conditions. Batches of eggs with single oil globules occurred most commonly. When oil globules were multiple, they were grouped together and not scattered throughout the yolk. The maximum number of oil globules observed was 12. Oil globules coalesced during egg development and it appeared that only one oil globule was present on newly hatched larvae. Egg diameter averaged 0.80 mm and ranged from 0.72 to 0.87 mm ($N = 265$). Oil globules, from eggs with one oil globule, averaged 0.21 mm in diameter and ranged from 0.18 to 0.28 mm ($N = 86$). The eggs hatched in about 48 h at 20° C.

[3]Hettler, W. F., A. B. Powell, and L. C. Clements. 1978. Laboratory induced spawning of spot, *Leiostomus xanthurus* (Lacepede). Annual Report of the Beaufort Laboratory to the U.S. Department of Energy, p. 351-356.

[4]Taylor, W. R., and G. C. Van Dyke. 1978. Staining and clearing small vertebraes for bone and cartilage study. Unpubl. manuscr., 19 p. National Museum of Natural History, Washington, DC 20560.

[5]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Early Stage Eggs

Pigment was never observed on the embryo or oil globule of early stage eggs. By the end of the early stage, when the blastopore was reduced to a small opening, optical vesicles were discernible, there were no visible myomeres, and the oil globule was situated adjacent to the blastopore, slightly posterior to the tail.

Middle Stage Eggs

Pigment first appeared on the embryo and oil globule during the middle stage (Figure 1A). Melanophores, which were mainly punctate, were scattered on the dorsal and lateral surface. Pigment was sparse or missing from the snout and on the posterior one-fourth of the body and was never present near the notochord tip. Melanophores appeared to be most dense in an area about one-third the body length from the snout. At the end of the middle stage, dendritic melanophores were more common and the pigment pattern was transitional from that illustrated for middle and late stage embryos (Figure 1). Also at this stage melanophores were relatively more dense on the dorsal surface of the head just posterior to the eyes and appeared to migrate laterally to form, eventually, a longitudinal row of dorsolateral melanophores. Initially, melanophores occurred on the posterior surface of the oil globule, but by the end of the middle stage they were located on the anterodorsal surface.

Late Stage Eggs

The embryos of late stage eggs developed a characteristic pigment pattern (Figure 1B) similar

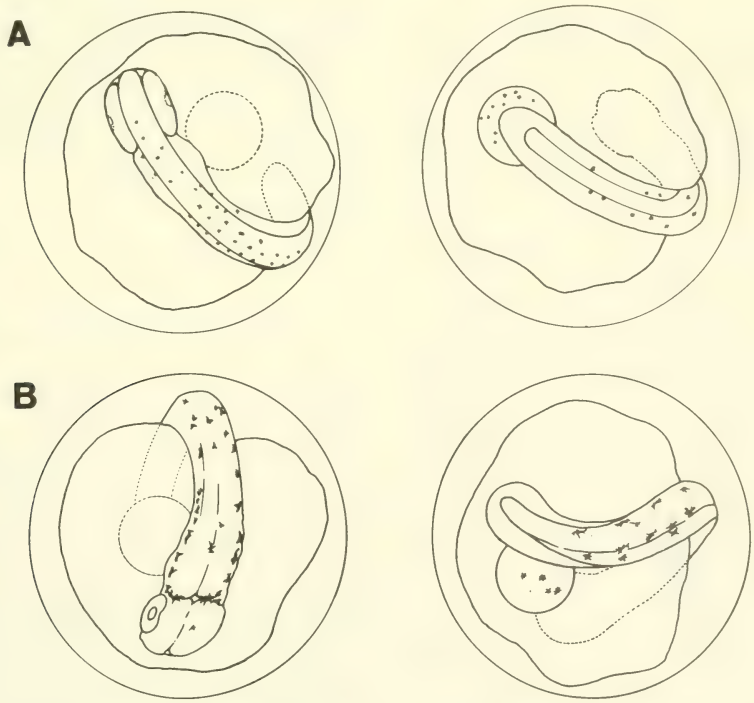


FIGURE 1.—Eggs of *Leiostomus xanthurus*: A, middle stage; left, the anterior part of embryo, right, the posterior part of embryo; B, late stage: left, the anterior part of embryo, right, the posterior part of embryo.

to that of Atlantic mackerel, *Scomber scombrus* (Berrien 1975). Melanophores on late stage eggs were relatively more dendritic than on earlier stage eggs. A row of dorsolateral melanophores on each side of the body extended from the posterior edge of the eyes posteriad. At about midbody, melanophores scattered over the dorsal surface disrupted this row of dorsolateral melanophores. Additional melanophores, which formed a transverse row across the head just posterior to the eyes were commonly observed. In the head region, anterior to the eyes and on the posterior portion of the body, melanophores were sparse. They were never observed on the posterior portion of the body near the notochord tip. Melanophores on the surface of the oil globule were located anteriorly.

Larval Development

Body Proportions

Newly hatched larvae measured 1.6-1.7 mm SL. A single oil globule was situated near the posterior margin of the yolk sac. The anterior portion of the body was arched over the yolk sac, but straightened out at ca. 2.0 mm SL (Figure 2). The yolk sac and oil globule were absorbed within 5 d at 20° C.

Most body proportions changed gradually during ontogeny except during very early development, when abrupt changes were observed. At this time, the head length, preanus length, body depth, and snout length became proportionately greater (Figures 3-5). On the other hand, the eye diameter, relative to the head length, became proportionately smaller with increasing body length (Figure 5A).

The most striking change in body shape was the development of the robust head which characterizes sciaenid larvae (Lippson and Moran 1974). This change, as revealed by an increase in the head length to body length ratio, occurred during the transition from the yolk sac to the preflexion stage, a time when little increase in body length occurred (Figure 3B).

Body proportions of larvae collected from the South Atlantic Bight (Powles and Stender 1978) and our laboratory-reared larvae are in good agreement, except that laboratory-reared larvae may be slightly more robust, especially those >7.0 mm SL. Fourteen percent of our laboratory-reared larvae (>7.0 mm SL) and 60% of our laboratory-reared juveniles (>14.4 mm SL) had body depths greater than the maximum (29.3%) reported by Powles and Stender (1978).

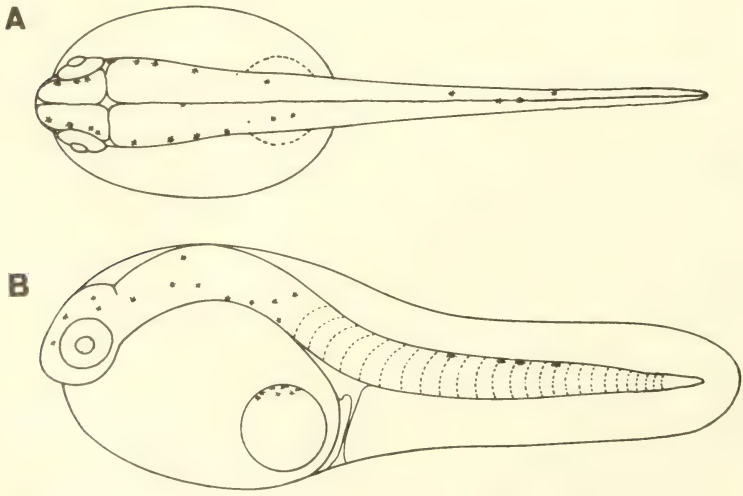


FIGURE 2.—Newly hatched *Leiostomus xanthurus*: A, dorsal view; B, lateral view.

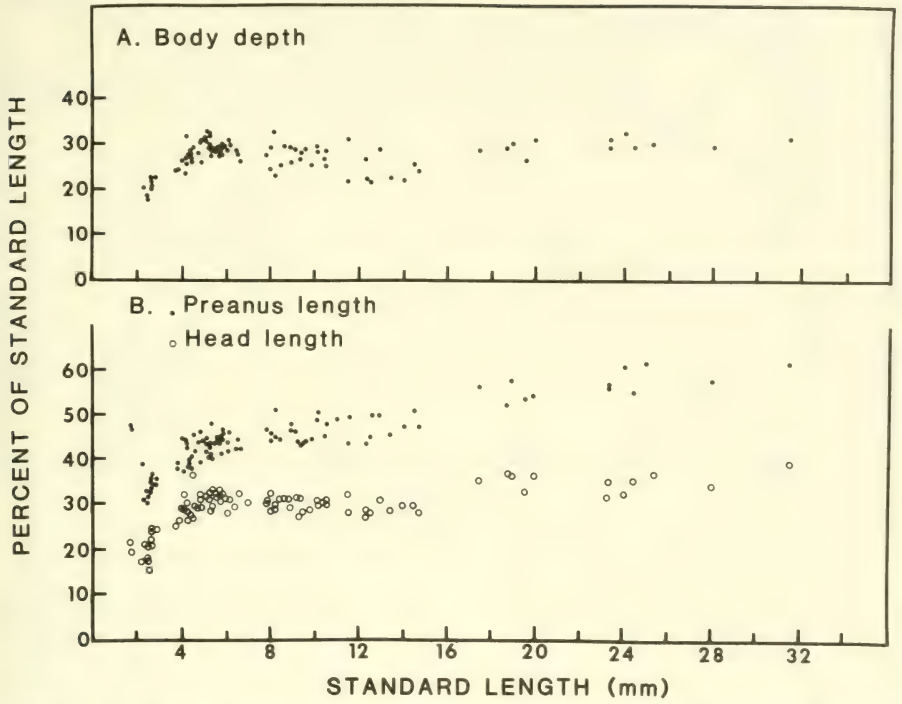


FIGURE 3.—Body proportions of *Leiostomus xanthurus* relative to the standard length: A, body depth; B, preanus length and head length.

Fin Development (Table 1)

Rayed fins initiated development in the following sequence: caudal, anal, second dorsal, first dorsal and pectoral, and pelvic. The adult complement of spines and rays was attained in the following sequence: principal caudal rays (9 upper + 8 lower), anal (II, 12-13), second dorsal (I, 29-35), first dorsal (IX-XI) and pelvic (I,5), secondary caudal rays (6-8 upper and lower), and pectoral (20-22).

A thickened area of tissue on the ventral side of the notochord was the first indication of caudal fin development (Figure 6). The rays began to form at the middle of the fin and developed dorsally and ventrally simultaneously. Principal caudal rays developed rapidly. They were first visible at 4.6 mm SL and by 65.3 mm SL the adult complement (9 upper + 8 lower), which is shared by all sciaenids, was reached. On the other hand, secondary caudal rays were slow to form. All specimens ≥14.4 mm SL had a complete caudal fin.

Dorsal fin rays started to form near the middle of the fin, between the 8th and 17th vertebrae, then developed anteriorly and posteriorly simultaneously. Soft rays were first observed at 6.7 mm SL. A full complement of second dorsal fin spines and soft rays was attained at 8.8 mm SL. A full complement of first dorsal fin spines was attained at 9.0 mm SL, and although the second dorsal on that particular larvae had a ray count within the adult range, the last soft ray was not formed. All specimens ≥10.8 mm SL had a complete dorsal fin. All our specimens had a first dorsal fin of 10 spines.

Anal fin rays started to form near the middle of the fin, between the 11th and 15th vertebrae, and then developed rapidly anteriorly and posteriorly. Soft rays were first observed at 6.3 mm SL and

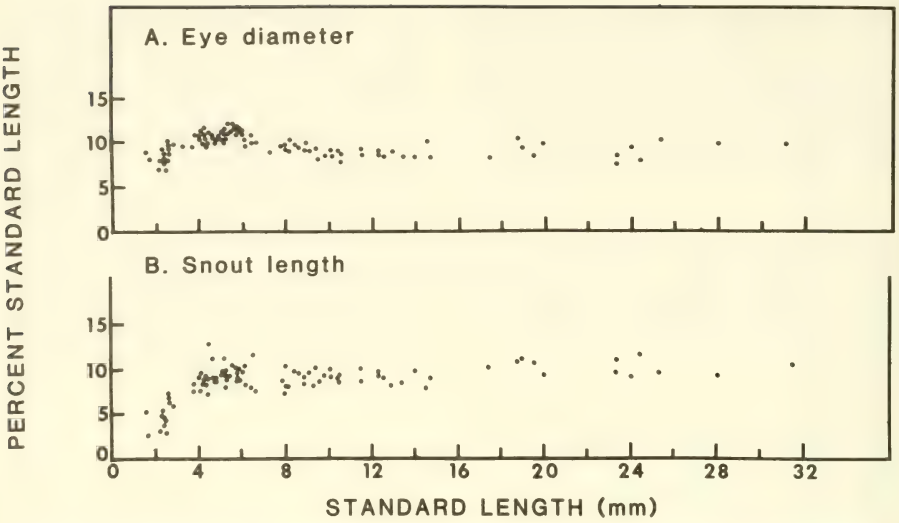


FIGURE 4.—Body proportions of *Leiostomus xanthurus* relative to the standard length: A, eye diameter; B, snout length.

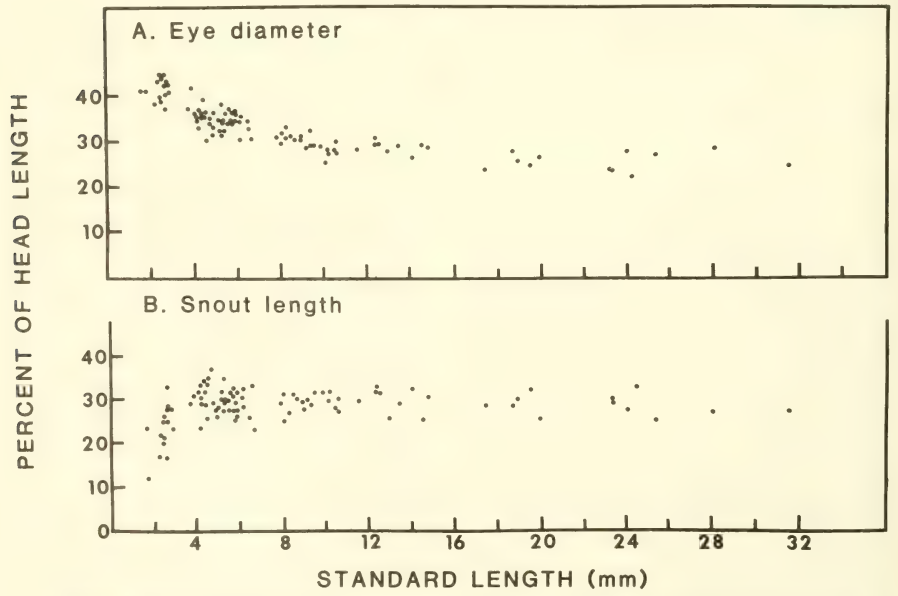


FIGURE 5.—Body proportions of *Leiostomus xanthurus* relative to the head length: A, eye diameter; B, snout length.

TABLE 1.—Meristic data from cleared and stained larval and juvenile *Leiostomus xanthurus*. Standard lengths suffixed with W indicate wild-caught specimens. All others are laboratory reared.

Standard length (mm)	Dorsal fin	Anal fin	Pelvic fin	Left pectoral fin[1]	Principal caudal rays[2]	Secondary caudal rays[2]	Branchiostegal rays	Gill rakers (left first arch) Epibranchial	Ceratobranchial	Hypobranchial
2.3	—	—	—	LF	—	—	—	—	—	—
2.7	—	—	—	LF	—	—	—	—	—	—
3.0	—	—	—	LF	—	—	—	—	—	—
3.7	—	—	—	LF	—	—	3	—	—	—
4.4	—	—	—	LF	—	—	5	—	—	—
4.6	—	—	—	LF	3+3	—	6	—	—	—
4.7	—	—	—	LF	—	—	6	—	—	—
5.1	—	—	Bud	LF	7+7	—	6	—	4	—
5.5	—	—	Bud	LF	7+7	—	6	—	4	—
5.5	—	—	Bud	LF	6+6	—	7	—	6	—
5.7	—	—	Bud	LF	8+7	—	6	—	6	—
6.3	—	6	Bud	LF	9+8	0+1	7	2	8	—
6.7	18	10	Bud	LF	9+8	1+1	7	1	8	—
6.8	14	7	Bud	LF	9+8	1+1	7	—	7	—
6.9	20	I,10	Bud	LF	9+8	1+2	7	2	8	—
7.9	23	I,11	Bud	LF	9+8	2+1	7	1	8	—
8.0	VIII,I,23	I,13	Bud	4	9+8	2+2	7	1	9	—
8.2	IX,I,26	II,12	I,3	7	9+8	2+2	7	3	11	—
8.4	IX,I,27	II,12	I,3	7	9+8	3+3	7	2	10	—
8.8	VIII,I,29	II,12	I,1	5	9+8	2+2	7	2	9	—
8.9	VIII,I,28	II,12	I,2	5	9+8	3+2	7	2	9	—
9.0	X,I,29	II,13	I,5	10	9+8	3+3	7	[3]	[3]	[3]
9.5	IX,I,30	II,12	Bud	5	9+8	2+2	7	2	9	—
9.7	IX,I,31	II,13	I,3	9	9+8	3+3	7	3	10	—
10.0	IX,I,31	II,12	I,4	10	9+8	3+2	7	3	10	—
10.8W	X,I,31	II,12	I,5	14	9+8	4+4	7	5	12	—
12.9	X,I,31	II,13	I,5	15	9+8	5+5	7	5	13	—
14.4	X,I,30	II,12	I,5	18	9+8	6+6	7	6	13	1
14.4	X,I,30	II,13	I,5	20	9+8	7+7	7	7	13	3
15.0	X,I,30	II,13	I,5	19	9+8	6+6	7	6	13	1
16.0	X,I,30	II,12	I,5	22	9+8	8+8	7	8	13	4
16.6W	X,I,31	II,12	I,5	20	9+8	7+7	7	8	13	2
17.7W	X,I,29	II,12	I,5	21	9+8	7+6	7	9	13	3
18.5W	X,I,31	II,12	I,5	21	9+8	7+7	7	7	13	4
19.1W	X,I,31	II,12	I,5	21	9+8	8+7	7	9	13	4
19.6W	X,I,29	II,12	I,5	21	9+8	7+7	7	9	13	4
20.1W	X,I,30	II,13	I,5	20	9+8	7+7	7	9	13	4
21.5W	X,I,31	II,12	I,5	22	9+8	7+7	7	8	13	5
48.0W	X,I,32	II,12	I,5	22	9+8	8+7	7	12	13	8

[1] LF designates larval fin.
[2] Upper + lower.
[3] Damaged.

spines at 6.9 mm SL. All specimens ≥8.2 mm SL had a completely developed anal fin.

The pelvic fin appeared as a bud at 5.1 mm SL. All specimens ≥10.8 mm SL had a completely developed pelvic fin. The fin formula I,5 is typical among sciaenids.

The pectoral, the last fin to develop a full complement of rays, persisted as a rayless blade for a relatively long period. Rays began to appear at 8.0 mm SL at the dorsal position of the blade and then developed ventrally. All specimens ≥16.0 mm SL had a complete pectoral fin.

Fin development, relative to body length of larvae, collected from the South Atlantic Bight (Powles and Stender 1978) was similar to fin development of laboratory-reared larvae, but spot larvae collected from the Gulf of Mexico (Fruge and Truesdale 1978) began and completed fin development at a much smaller size (Table 2). Rate of fin development could be influenced by temperature. Size at hatching, at least, has been shown to be influenced by incubation temperature (Laurence and Rogers 1976).

TABLE 2.—The size (mm SL) when fins and associated structures begin and complete development for laboratory-reared spot (this study), spot collected from the South Atlantic Bight (Powles and Stender 1978) and spot collected from the Gulf of Mexico (Fruge and Truesdale 1978).

Fin or associated structure	Begins formation: Powles and Stender (1978)	Fruge and Truesdale (1978)	This study	Completes formation: Powles and Stender (1978)	Fruge and Truesdale (1978)	This study
Notochord flexion	4.4	4-5	3.8	4.7	4-5	5.3
Caudal fin:						
Principal rays	4.5	3	4.6	7.2	5	6.3
Secondary rays	6.2	5	6.3	15.5	>10.7	14.4
Anal fin pterygiophores	4.4	—	5.5	6.2	—	6.3
Anal fin	7.2	5	6.3	9.3	7	8.2
Dorsal fin:						
Pterygiophores	4.4	—	5.1	—	—	7.3
Second	7.2	5	6.7	9.3	8	8.8
First	7.2	7	8.0	14.1	9	10.8
Pelvic fin bud	5.2	5-6	5.1	—	—	—
Pelvic fin	8.0	6	8.2	10.7	7-9	10.8
Pectoral fin	10.7	7	8.0	16.8	>10.7	16.0

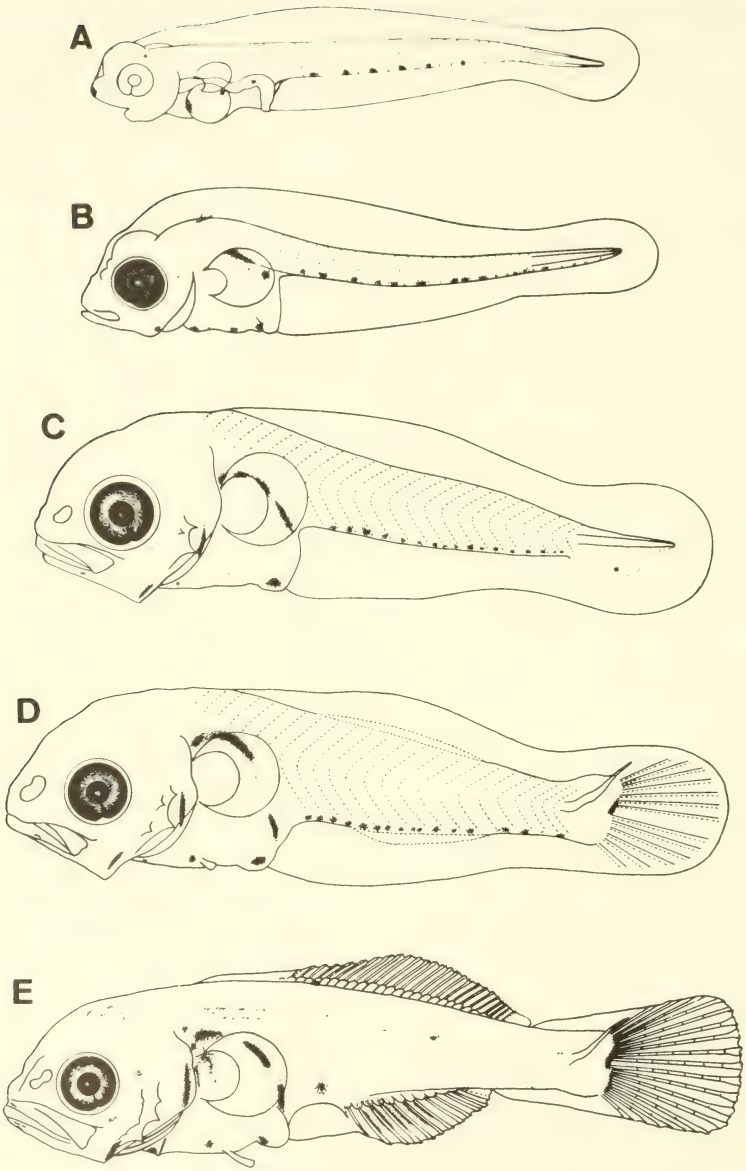


FIGURE 6.—Developmental stages of *Leiostomus xanthurus*: A, 2.4 mm SL late yolk-sac larva; B, 2.6 mm SL preflexion larva; C, 4.1 mm SL early-flexion larva; D, 5.2 mm SL postflexion larva; E, 8.0 mm SL postflexion larva.

Pterygiophore Development and Arrangements

Fully developed spot had three predorsal bones which did not support spines (Figure 7): One such bone was located between the skull and first neural spine, one between the first and second neural spines, and one between the second and third neural spines. They began to develop at 5.7 mm SL, anteroposteriorly, and the full complement was recognizable at 8.2 mm SL (Figure 8).

There were two fewer pterygiophores than dorsal fin elements (spines and soft rays) on fully developed spot. The anteriormost pterygiophore was associated with three spines (Figure 7). It was secondarily associated with the first two spines and serially associated with the third spine. All other pterygiophores were serially associated with one dorsal fin element and secondarily associated with a preceding element.

Dorsal fin pterygiophores were first apparent at 5.1 mm SL between neural spines 9 through 14 and development proceeded anteriorly and posteriorly simultaneously (Figure 8). The adult complement was achieved at 8.2 mm SL.

Although there was a variable number of dorsal pterygiophores between neural spines (Table 3), a nearly consistent pattern was observed (Figure 7). The formula[6]

P / P / P+1 / 2 / 1 / 2 / 1 / 2 / 2 /

[6]Each P represents a predorsal bone, each slant a neural spine and the numerals indicate the number of pterygiophores between neural spines.

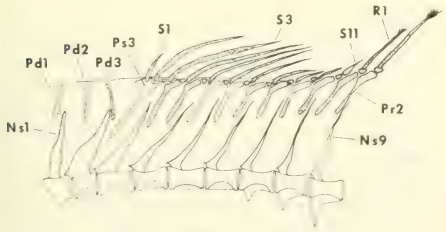


FIGURE 7.—Arrangement of predorsal bones, and the first 11 dorsal fin pterygiophores in relation to neural spines for *Leiostomus xanthurus* (19.6 mm SL). Spine S11 is the first spine of the second dorsal fin. Ps3, represents the pterygiophore in serial association with the third dorsal spine; Pr2, the pterygiophore in serial association with the second ray of the second dorsal fin; S1, the first spine on the first dorsal fin; R1, the first ray on the second dorsal fin; Ns1, the neural spine on the first centrum; and Pd, the predorsal bones.

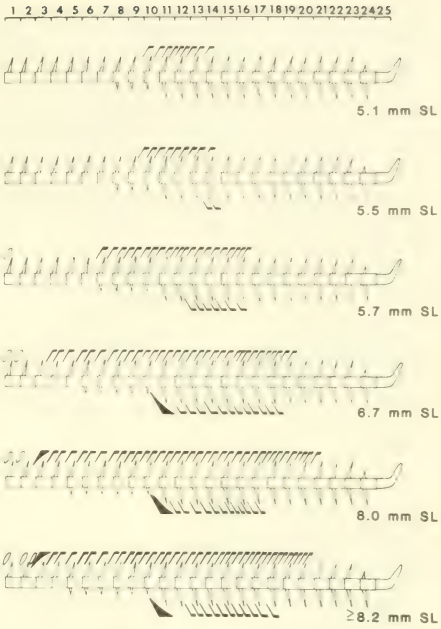


FIGURE 8.—Schematic representation of the development of predorsal bones (unshaded), and dorsal and anal fin pterygiophores (darkened) in *Leiostomus xanthurus*.

TABLE 3.—Frequencies of dorsal fin pterygiophores between neural spines in 23 *Leiostomus xanthurus* (8.2-48.0 mm SL).

Neural spine number	No. of pterygiophores between neural spines					Neural spine number	No. of pterygiophores between neural spines				
	0	1	2	3	4		0	1	2	3	4
2-3	—	23	—	—	—	12-13	—	—	19	4	—
3-4	—	1	22	—	—	13-14	—	—	17	6	—
4-5	—	22	1	—	—	14-15	—	—	10	13	—
5-6	—	1	22	—	—	15-16	—	—	15	8	—
6-7	—	21	2	—	—	16-17	—	—	11	12	—
7-8	—	—	23	—	—	17-18	—	—	9	14	—
8-9	—	—	23	—	—	18-19	—	—	2	21	—
9-10	—	1	20	2	—	19-20	—	1	—	16	6
10-11	—	—	21	2	—	20-21	11	9	2	—	1
11-12	—	—	13	10	—						

occurred in 87% of our 23 specimens. We also observed that in 96% of those specimens the anteriormost pterygiophore between neural spines 7 and 8 was serially associated with the last spine of the first dorsal fin (Figure 7).

Fully developed spot had two fewer pterygiophores than anal fin elements. Like the dorsal fin, the anteriormost anal fin pterygiophore was as-

sociated with three elements (Figure 9). It was secondarily associated with the first two spines and serially associated with the first ray. All other pterygiophores were serially associated with one anal fin ray and secondarily associated with a preceding ray. In the largest specimen (48.0 mm SL) a stay was associated with the last anal fin pterygiophore.

The number of anal fin pterygiophores between haemal spines was highly variable. The first pterygiophore, however, always occurred, singly, between the last precaudal vertebra (number 10) and the first caudal vertebra (number 11) (Table 4).

Anal fin pterygiophores were first observed at 5.5 mm SL (Figure 8). Development began between haemal spines 3 and 4 and proceeded anteriorly and posteriorly simultaneously. Development was rapid. The adult complement was reached at 6.3 mm SL.

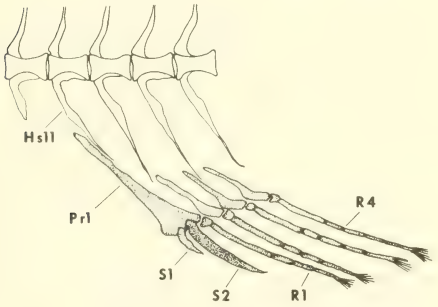


FIGURE 9.—Arrangement of the first four anal fin pterygiophores in relation to haemal spines for *Leiostomus xanthurus* (19.6 mm SL). Pr1, pterygiophore in serial association with the first anal fin ray; Hs11, the first haemal spine on the 11th centrum; S, anal spine; R, anal ray.

Other Structures

Centra were not fully differentiated until ca. 9 mm SL, but the adult complement of vertebrae (25, including urostyle) was determined from larvae as small as 4.6 mm SL by counting combinations of neural spines and myosepta (Figure 10A). Precaudal vertebrae (10) were differentiated from caudal vertebrae (15) in larvae as small as 5.1 mm SL (Figure 10B). The first caudal vertebra was easily identified as its haemal spine was approximately three times longer than the preceding parapophysis.

TABLE 4.—Frequencies of anal fin pterygiophores between haemal spines in 30 *Leiostomus xanthurus* (5.7-40.8 mm SL).

Haemal spine number	No. of pterygiophores between haemal spines				Haemal spine number	No. of pterygiophores between haemal spines			
	0	1	2	3		0	1	2	3
10-11	—	30	—	—	14-15	—	1	28	1
11-12	19	10	1	—	15-16	—	—	28	2
12-13	—	9	21	—	16-17	—	—	22	8
13-14	—	1	29	—	17-18	9	14	7	—

One important adult characteristic of the genus *Leiostomus* is an entire preopercular margin. Spot larvae and early juveniles, however, exhibited preopercular, subopercular, and interopercular spines (Figure 11). Preopercular spines formed first (4.4 mm SL). They occurred in two rows, one of weak lateral spines and one of stouter marginal spines. Preopercular spines increased during ontogeny, but juveniles eventually lost these spines. Interopercular and subopercular spines are less important characters for larval identification because they formed during the late larval period (Figure 11). They also were lost during the early juvenile stage.

Branchiostegal rays appeared early in development and attained the adult complement (7), shared by all sciaenids, at 6.3 mm SL (Table 1).

Spot have a high number of gill rakers among sciaenids (29-36, Chao and Musick 1977), but since the adult complement was not attained until a large size was reached (Table 1), total gill raker counts were not considered to be a good diagnostic character. The full complement of gill rakers on the ceratobranchial, however, was obtained at ca. 13 mm SL.

Pigmentation

Newly hatched larvae were inconspicuously pigmented (Figure 2). An ill-defined row of faint melanophores on the anterior portion of the body extended from the anterodorsal surface of the head to the ventrolateral surface of the trunk. Posterior to the anus on the dorsal midline, there were about two to five faint punctate melanophores. Faint melanophores occurred on the anterodorsal surface of the oil globule.

Shortly after hatching (ca. 1 d), a characteristic pattern began to form on the body. Initially, on almost all larvae, there was a faint dorsal and ventral melanophore opposite each other, located about midbody. In addition, there were other faint melanophores which, initially, occurred mainly on the dorsal midline. With larval growth, there were

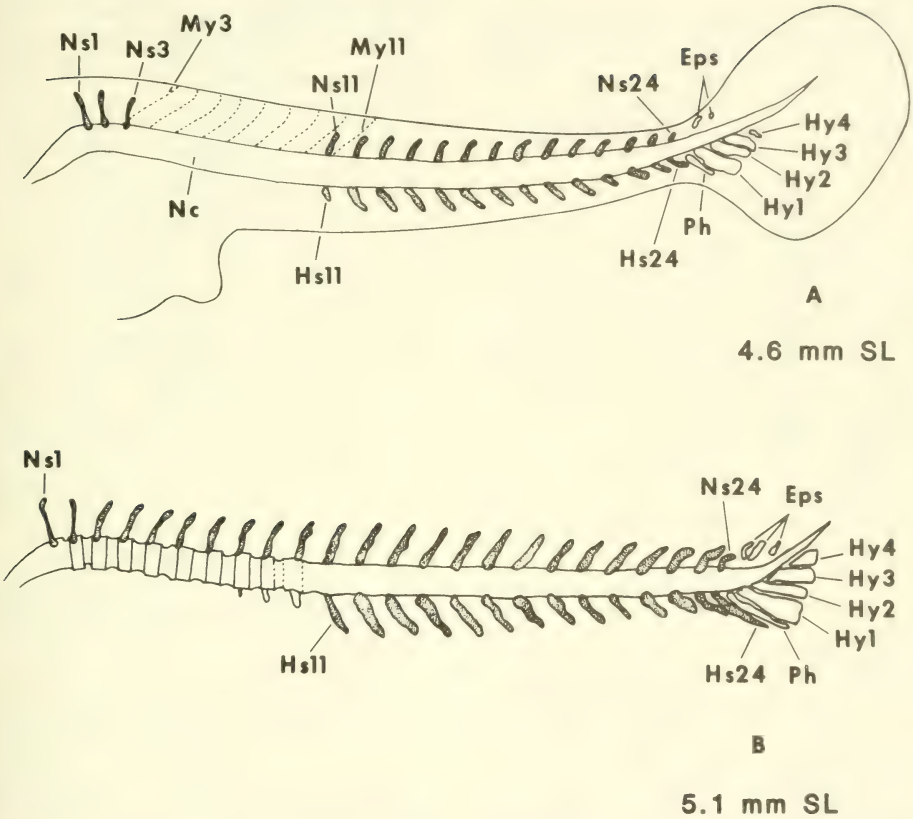


FIGURE 10.—Parts of axial skeleton used in counting: (A) total vertebrae (only myosepta useful in counting vertebrae are shown) and (B) precaudal and caudal vertebrae in *Leiostomus xanthurus* early larvae. Ns, neural spine; Hs, haemal spine; My3, myosepta associated with the third neural spine; Ph, parhypural; Hy, hypural bone; Eps, epurals; Nc, notochord.

fewer dorsal melanophores and more ventral melanophores. Finally, at the late yolk-sac stage (Figure 6A) a characteristic body pigment pattern was established (i.e., a single row of melanophores along the ventral midline) that persisted throughout the larval period.

Distinguishing characteristics of postyolk-sac spot larvae have been reported (Fruge and Truesdale 1978; Powles and Stender 1978), but the size or stage when spot larvae acquire these characteristics has generally been unknown. After yolk-sac absorption, there were five characteristic pigmented areas that developed in the region of the head and abdomen (Figure 6B-E)

1. Embedded melanophores over the air bladder and hindgut. They were observed on the youngest preflexion larvae (2.3 mm SL).
2. A triangle on the ventral side of the abdomen composed of a well-defined melanophore just anterior to the anus and a faint melanophore at each future pelvic fin base, although one was lacking at times (see Lippson and Moran 1974 for illustration), This pattern was occasionally

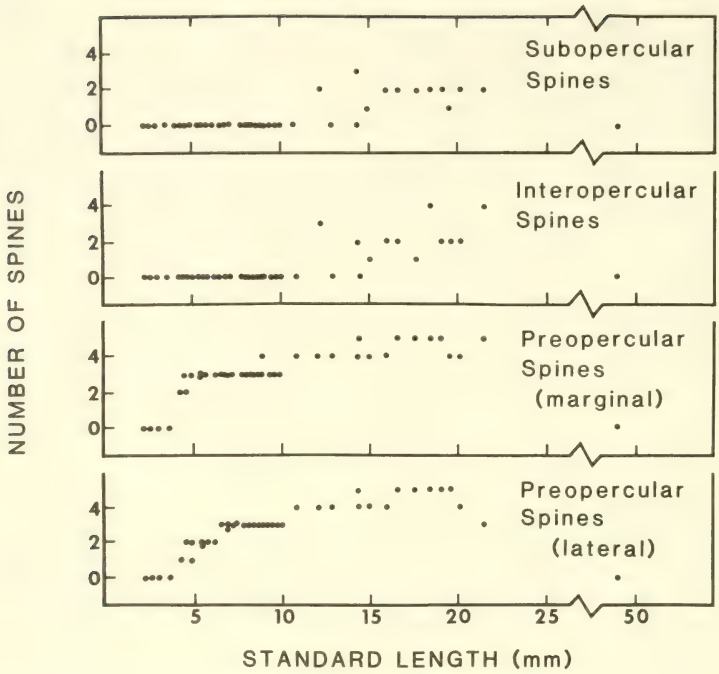


FIGURE 11.—Frequency of preopercular, interopercular, and subopercular spines in *Leiostomus xanthurus*.

observed on preflexion larvae and on almost all older larvae.

3. A well-defined melanophore at the cleithral symphysis on the ventral side of the abdomen. This melanophore first appeared on flexion larvae (3.8 mm SL).
4. A melanophore at the lower jaw angle first appeared on preflexion larvae (2.6 mm SL).
5. Embedded pigment at the anterior of the gut between the left and right cleithrum first became apparent on flexion larvae (4.0 mm SL), but were seen on cleared and stained late preflexion larvae (2.9 mm SL).

Two other characteristic pigment patterns were observed on the body: 1) a faint melanophore at the base of the caudal fin first appeared on most early flexion larvae (Figure 6C); then additional melanophores were added (Figure 6D) which eventually outlined the base of the caudal fin (Figure 6E), and 2) imbedded melanophores on the perineural sheath appeared at ca. 6-7 mm SL (Figure 6E).

Distinguishing Spot from Other Sciaenids

The eggs and larvae of most sciaenids are not likely to occur with spot eggs and larvae since the spawning seasons and localities of these sciaenids and spot do not overlap (Guest and Gunter 1958; Johnson 1978; Powles and Stender 1978). Spot, which spawns in continental shelf waters during the winter, share this spawning locality with *Cynoscion nothus*, *Equetus* spp., *Larimus fasciatus*, and *Micropogonias undulatus*. Of these sciaenids, only the Atlantic croaker appears to share the same spawning season with spot (the spawning season of *Equetus* spp. is unknown). The eggs and early preflexion larvae of Atlantic croaker have not been described and, therefore,

cannot presently be separated from spot, but distinguishing characteristics useful in separating older larvae are well documented (Fruge and Truesdale 1978; Powles and Stender 1978). During late fall and early spring, eggs and early larvae of *L. fasciatus* and *C. nothus* could occur with those of spot (Berrien et al. 1978; Powles and Stender 1978). The eggs of both these species are undescribed, whereas their larvae bear no resemblance to spot larvae (Powles and Stender 1978).

Meristic characters are useful in separating spot larvae from those of other sciaenids (Table 5). Flexion and older stage spot can be separated from *C. nothus*, which may be the only species of *Cynoscion* whose eggs and early larvae occur with spot, by total vertebrae counts. *Cynoscion nothus* has 27, rarely 26 vertebrae (high for sciaenids); spot has 25. Beginning at ca. 5 mm SL, spot can be separated from all members of the genus *Cynoscion* inhabiting the western North Atlantic by the number of precaudal vertebrae. *Cynoscion* spp. have more precaudal vertebrae (13-15) than spot (10).

The arrangement of predorsal bones and pterygiophores can be important in determining phylogenetic relationships (Kendall 1976) and in distinguishing between closely related species (Potthoff 1974; Berrien 1978; Butler 1979).

TABLE 5.—Meristic characters useful for separating spot larvae from other sciaenids. Check (√) indicates nonoverlapping counts, dash (—) indicates overlapping counts. Meristics were obtained from cleared and stained specimens.

Species	Meristic character and (in parenthesis) the size (mm SL) at which spot attained the full complement in this study			
	Total vertebrae (4.6)	Precaudal + caudal vertebrae (5.1)	Anal fin[1] pterygiophores (6.3)	Dorsal fin[2] pterygiophores (7.3)
Bairdiella chrysoura	—	—		
Cynoscion arenarius	—		—	√
C. nebulosus	—	√	—	—
C. nothus		√		—
C. regalis	—	√	—	—
Larimus fasciatus	—	—	√	—
Menticirrhus americanus	—	—	√	√
M. littoralis	—	—	√	√
M. saxatilis	—	—	√	√
Micropogonias undulatus	—	—		—
Pogonias cromis		√		√
Sciaenops ocellata	—	—	√	√
Stellifer lanceolatus	—	—		

[1]The full complement of anal fin spines and rays was attained at 8.2 mm SL.
[2]The full complement of dorsal fin spines and rays was attained at 10.8 mm SL.

Pterygiophores are important larval meristic characters, since their full complement is attained before accompanying spines and rays are formed. Since spot have high anal fin ray counts among sciaenids, then anal fin pterygiophore counts would be of utmost importance in separating spot larvae from other sciaenid larvae (Table 5).

ACKNOWLEDGMENTS

We are most grateful to Howard Powles (Environment Canada, Quebec, Canada) and William R. Nicholson, Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOAA, who reviewed an earlier draft of this manuscript and offered valuable comments and criticism, and to William Hettler (Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOAA) for his valuable contributions to our larval fish rearing program. This research was supported by an interagency agreement between the National Marine Fisheries Service and the Department of Energy.

LITERATURE CITED

AHLSTROM, E. H., AND O. P. BALL.
1954. Description of eggs and larvae of jack mackerel (*Trachurus symmetricus*) and description and abundance of larvae in 1950 and 1951. U.S. Fish Wildl. Serv., Fish. Bull. 56:209-245.

AHLSTROM, E. H., J. L. BUTLER, AND B. Y. SUMIDA.
1976. Pelagic stromateoid fishes (Pisces, Perciformes) of the Eastern Pacific: kinds, distributions, and early life histories and observations on five of these from the Northwest Atlantic. Bull. Mar. Sci. 26:285-402.

APRIETO, V. L.
1974. Early development of five carangid fishes of the Gulf of Mexico and the south Atlantic coast of the United States. Fish. Bull., U.S. 72:415-443.

BERRIEN, P. L.
1975. A description of Atlantic mackerel, *Scomber scombrus*, eggs and early larvae. Fish. Bull., U.S. 73:186-192.
1978. Eggs and larvae of *Scomber scombrus* and *Scomber japonicus* in continental shelf waters between Massachusetts and Florida. Fish. Bull., U.S. 76:95-115.

BERRIEN, P. L., M. P. FAHAY, A. W. KENDALL, JR., AND W. G. SMITH.
1978. Ichthyoplankton from the RV *Dolphin* survey of Continental Shelf waters between Martha's Vineyard, Massachusetts and Cape Lookout, North Carolina, 1965-1966. U.S. Natl. Mar. Fish. Serv., Northeast Fish. Cent., Sandy Hook Lab., Tech. Ser. Rep. 15, 152 p.

BUTLER, J. L.
1979. The nomeid genus *Cubiceps* (Pisces) with a description of a new species. Bull. Mar. Sci. 29:226-241.

CHAO, L. N.
1978. A basis for classifying western Atlantic Sciaenidae

(Teleostei: Perciformes). U.S. Dep. Commer., NOAA Tech. Rep. NMFS Circ. 415, 64 p.

CHAO, L. N., AND J. A. MUSICK.
1977. Life history, feeding habits, and functional morphology of juvenile sciaenid fishes in the York River estuary, Virginia. Fish. Bull., U.S. 75:657-702.

DINGERKUS, G., AND L. D. UHLER.
1977. Enzyme clearing of alcian blue stained whole small vertebrates for demonstration of cartilage. Stain Technol. 52:229-232.

FAHAY, M. P.
1975. An annotated list of larval and juvenile fishes captured with surface-towed meter net in the South Atlantic Bight during four RV *Dolphin* cruises between May 1967 and February 1968. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-685, 39 p.

FRUGE, D. J., AND F. M. TRUESDALE.
1978. Comparative larval development of *Micropogon undulatus* and *Leiostomus xanthurus* (Pisces: Sciaenidae) from the northern Gulf of Mexico. Copeia 1978:643-648.

GUEST, W. C., AND G. GUNTER.
1958. The seatrout or weakfishes (genus *Cynoscion*) of the Gulf of Mexico. Gulf States Mar. Fish. Comm., Tech. Summ. 1, 40 p.

HETTLER, W. F.
1979. Modified neuston net for collecting live larval and juvenile fish. Prog. Fish-Cult. 41:32-33.

HILDEBRAND, S. F., AND L. E. CABLE.
1930. Development and life history of fourteen teleostean fishes at Beaufort, N.C. Bull. U.S. Bur. Fish. 46:383-488.
1934. Reproduction and development of whitings or kingfishes, drums, spot, croaker, and weakfishes or sea trouts, family Sciaenidae, of the Atlantic coast of the United States. Bull. U.S. Bur. Fish. 48:40-117.

HOUDE, E. D., AND T. POTTHOFF.
1976. Egg and larval development of the sea bream *Archosargus rhomboidalis* (Linnaeus): Pisces, Sparidae. Bull. Mar. Sci. 26:506-529.

JOHNSON, G. D.
1978. Development of fishes of the Mid-Atlantic Bight, vol. 4. U.S. Fish. Wildl. Serv., Biol. Serv. Program, Wash., D.C., 314 p.

KENDALL, A. W., JR.
1976. Predorsal and associated bones in serranid and grammistid fishes. Bull. Mar. Sci. 26:585-592.

LAURENCE, G. C., AND C. A. ROGERS.
1976. Effects of temperature and salinity on comparative embryo development and mortality of Atlantic cod (*Gadus morhua* L.) and haddock (*Melanogrammus aeglefinus* (L.)). J. Cons. 36:220-228.

LIPPSON, A. J., AND R. L. MORAN.
1974. Manual for identification of early developmental stages of fishes of the Potomac River Estuary. Md. Dep. Nat. Resour., Baltimore, 282 p.

NELSON, W. R.
1969. Studies on the croaker, *Micropogon undulatus* Linnaeus, and the spot, *Leiostomus xanthurus* Lacepede, in Mobile Bay, Alabama. J. Mar. Sci. (Ala.) 1:4-92.

PEARSON, J. C.
1929. Natural history and conservation of redfish and other commercial sciaenids on the Texas coast. Bull. U.S. Bur. Fish. 44:129-214.

POTTHOFF, T.
1974. Osteological development and variation in young tunas, genus *Thunnus* (Pisces, Scombridae), from the Atlantic Ocean. Fish. Bull., U.S. 72:563-588.

POWLES, H., AND B. W. STENDER.
1978. Taxonomic data on the early life history stages of Sciaenidae of the South Atlantic Bight of the United States. S.C. Mar. Resour. Cent. Tech. Rep. 31, 64 p.

BOMOLOCHID COPEPODS PARASITIC ON THE EYES OF INDO-WEST PACIFIC CLUPEID FISHES

ROGER CRESSEY AND HILLARY BOYLE CRESSEY[1]

ABSTRACT

Three genera of bomolochid copepods (*Pumiliopes*, *Pumiliopsis*, *Pseudorbitacolax*) parasitic on the eyes of Indo-West Pacific clupeid fishes are redefined. *Pseudorbitacolax fimbriatus* new species is described, *Pseudorbitacolax varunae* (Bennet) is redescribed, *Orbitacolax nudus* Cressey and Boyle is transferred to the genus *Pseudorbitacolax*, *Pumiliopsis emarginatus* Cressey and Boyle is placed in synonymy with *Pumiliopsis sardinellae* (Bennet), and *Pumiliopes capitulatus* Cressey and Boyle is placed in synonymy with *Pumiliopes jonesi* (Bennet). Included also is a key to the genera of bomolochid copepods parasitic on the eyes of Indo-West Pacific clupeids and scanning electron micrographs of three species.

In 1973 we described five new bomolochid copepods collected from the eyes of Indo-West Pacific clupeid fishes housed in the Smithsonian (USNM) collections. Since then we have collected more copepods (including one new species) from clupeids in the collections of the Museum of Comparative Zoology at Harvard University (MCZ) and the British Museum (Natural History) (BM).

Examination of these additional collections (Table 1) enabled us to redescribe the three genera of bomolochids (*Pumiliopes*, *Pumiliopsis*, *Pseudorbitacolax*) parasitic on the eyes of Indo-West Pacific clupeid hosts, to transfer *Orbitacolax nudus* Cressey and Boyle to the genus *Pseudorbitacolax* Pillai, and to place *Pumiliopsis emarginatus* Cressey and Boyle in synonymy with *Pumiliopsis sardinellae* (Bennet), and to place *Pumiliopes capitulatus* Cressey and Boyle in synonymy with *Pumiliopes jonesi* (Bennet). This paper also includes scanning electron micrographs of some species and a summary of the results of our later collections.

[1]Department of Invertebrate Zoology, Smithsonian Institution, Washington, DC 20560.

TABLE 1.—Indo-West Pacific clupeids and the copepods parasitic on their eyes.

Host	Parasite
Anodontostoma chacunda	*Pseudorbitacolax varunae*
Clupanodon punctatus	*Pumiliopes jonesi*
Herklotsichthys dispionotus	*P. jonesi*
H. punctatus	*Pseudorbitacolax nudus*
Sardinella albella	*Pumiliopsis sardinellae*
S. bulan	*P. sardinellae*
S. fimbriata	*Pumiliopes squamosus*
	Pumiliopsis sardinellae
	Pseudorbitacolax fimbriatus
S. jussieui	*Pumiliopes squamosus*
	Pumiliopsis sardinellae
S. sirm	*P. plautus*
S. zunasi	*Pumiliopes squamosus*

Manuscript accepted December 1979.
FISHERY BULLETIN: VOL. 78, NO. 3, 1980.

Key to the Genera of Female Bomolochids Parasitic on the Eyes of Indo-West Pacific Clupeid Fishes

1a. Legs 2-4 exopods 2-segmented 2
1b. Legs 2-4 exopods 3-segmented ..... *Pseudorbitacolax*
2a. Legs 2-4 exopod last segment with barbed or serrate spine ..... *Pumiliopsis*
2b. Legs 2-4 exopod last segment with smooth, clawlike spine ..... *Pumiliopes*

Pseudorbitacolax Pillai 1971

Diagnosis.—Bomolochidae. Female: Body dorsoventrally flattened. Rostrum rounded or bilobed. Abdomen 2- or indistinctly 3-segmented. Caudal rami each with one long, five short setae. First antenna with no modified setae. Last segment of second antenna with few to many hooklets, four hooked spines, and two setae terminally. Maxilliped claw with no outer accessory process. Legs 1-4 biramous. Leg 1 flattened, rami 2-segmented. Rami of legs 2-4 3-segmented, last segment of exopods each with apical barbed or serrate spine. Second endopod segment of leg 2 with two inner setae. Second endopod segment of legs 3 and 4 each with one inner seta.

Male.—Rostrum slightly produced, broader than long. Thoracic segments each slightly narrower than preceding segment. Genital segment longer than broad. Abdomen 2-segmented. Caudal rami each with one very long and five shorter setae. First antenna extending beyond margins of cephalothorax, with numerous long slender setae. Second segment of maxilliped ornamented on inner surface with numerous small, knoblike spinules, one long seta, and a row of short spinules; terminal segment in form of a claw armed with stout teeth along entire inner margin apposing second segment. Legs 1-4 biramous, rami 3-segmented except endopod of leg 4 2-segmented. Leg 1 endopod flattened. Second endopod segment of legs 2 and 3 each with two inner setae.

Type-species.—*Pseudorbitacolax varunae* (Bennet 1966).

Remarks.—In placing two more species in this genus we have been able to modify Pillai's (1971) original generic diagnosis, especially with regard to the size and shape of the rostrum and the first maxilla. As with *Pumiliopsis*, the structure of the rostrum is a specific rather than a generic character. The three setae of the first maxilla are of variable lengths rather than all small as stated by Pillai.

Our diagnosis of the male is based on a single, damaged specimen of *Pseudorbitacolax fimbriatus* and, as such, must be considered tentative until additional material is collected.

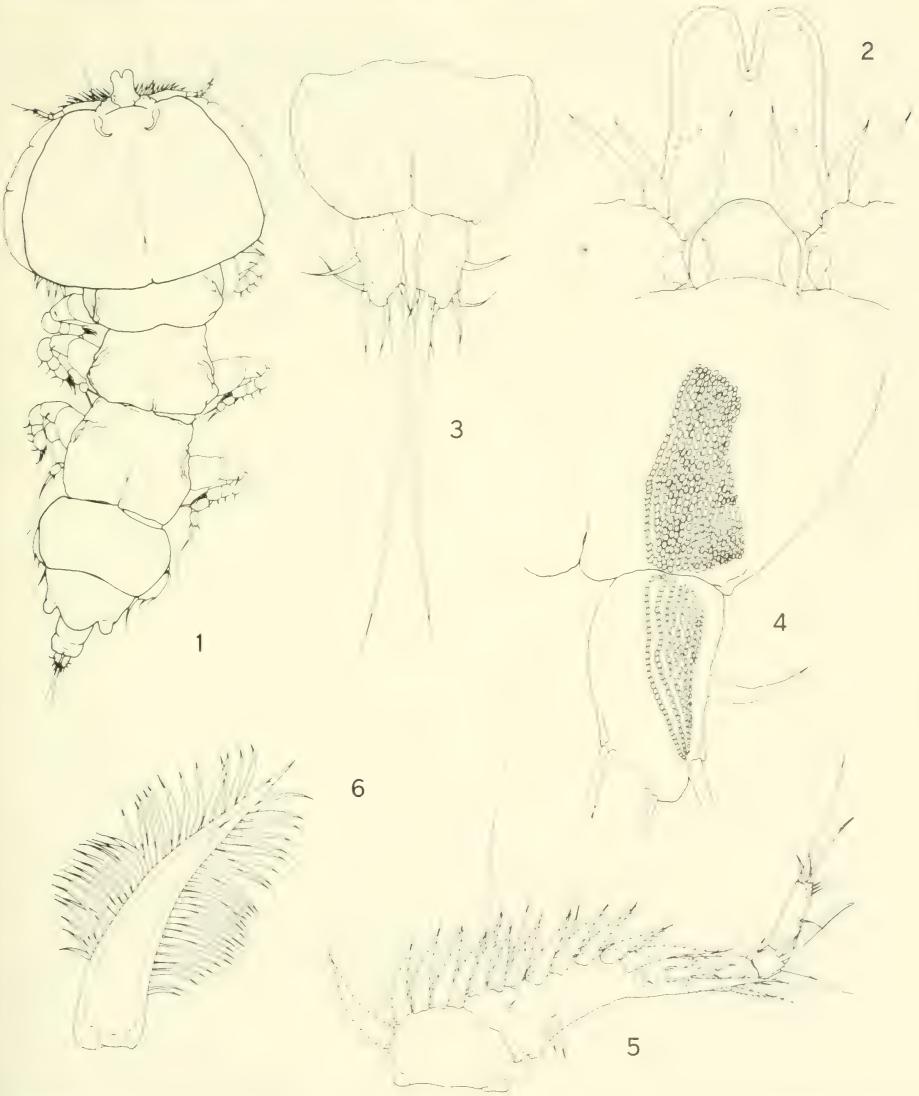
Pseudorbitacolax fimbriatus new species (Figures 1-17)

Material examined.—Two collections containing 3 ♀ 1 ♂ (holotype ♀ USNM 173021, allotype ♂ USNM 173022, two paratype ♀ USNM 173023) from the eyes of two *Sardinella fimbriata* (BM 1972.9.5.22, BM 1972.9.5.25) from New Guinea.

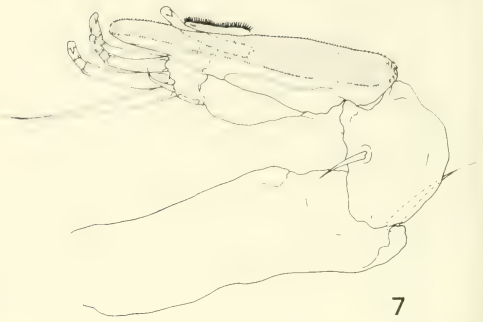
Female.—Body form as in Figure 1. Total length 3.66 mm, greatest width 1.60 mm (measured at widest part of cephalothorax). Cephalothorax length 1.42 mm and with lateral marginal membranes. Rostrum (Figure 2) with bilobed tip, each lobe gently rounded, with two dorsal hooks near base; rostrum length 236 μm, width at base 206 μm. Genital segment (see Figure 1) wider than long (389 × 601 μm) with a greatly rounded process at each outer distal corner. Abdomen 2-segmented: first segment wider than long (118 × 224 μm) without ornamentation; second segment wider than long (94 × 200 μm) with two ventral patches of scalelike spinules arranged in uneven longitudinal rows (see Figures 3 and 4). Caudal rami (Figure 3) longer than wide (82 × 53 μm); each ramus with a patch of scalelike spinules in rows (Figure 4) and six setae (longest seta 289 μm).

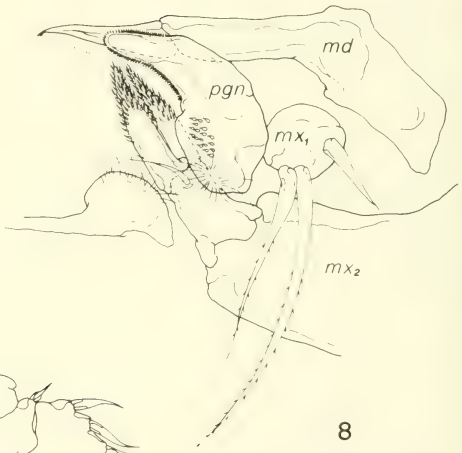
First antenna (Figure 5) 5-segmented: basal two segments with 9 naked and 15 plumose setae; latter with broad, flattened plumosities (Figure 6); an aesthete present on each of last two segments. Second antenna (Figure 7) with several rows of minute spinules on third segment, four hooked spines, and two setae distally. Labrum with two large patches of scalelike spinules. Mandible, paragnath, first maxilla, and second maxilla as in Figure 8. Labium represented as a small, rounded, hairy lobe posterior to mouth. Base of maxilliped (Figure 9) posterior to oral area, armed with four setae and a strongly curved hook without an accessory process.

Legs 1-4 biramous, rami of legs 2-4 3-segmented. Leg 1 (Figure 10) interpodal plate with two patches of scalelike spinules; coxopod with broad inner seta; basipod with two patches of scalelike spinules; exopod first segment with outer spine, second segment with two naked and seven plumose setae; endopod first segment with outer patch of scalelike spinules and inner plumose seta, second segment with outer patch of scalelike spinules and six plumose setae; outer edges of endopod heavily hirsute. Basipod of leg 2 (Figure 11) with large ventral patch of scalelike spinules and a short dorsal seta; first segment of exopod with patch of scalelike spinules (Figure 11a) covering most of segment and one spine on outer distal corner, second segment with outer spine and outer patch of minute pointed spinules (Figure 11b), third segment with two outer spines, one barbed terminal spine and three inner setae, outer portion of segment with two distinct patches of spinules similar to those on second segment; first segment of endopod with minute, barely perceptible inner seta and a large patch of scalelike spinules, outer edge of segment fringed with short, blunt hairs, second segment with two inner setae and outer patch of scalelike spinules, outer edge of segment fringed with short hairs, third segment with two inner setae, one terminal spine and outer to terminal patch of scalelike spinules. Basipod of leg 3 (Figure 12) with dorsal seta, exopod and first

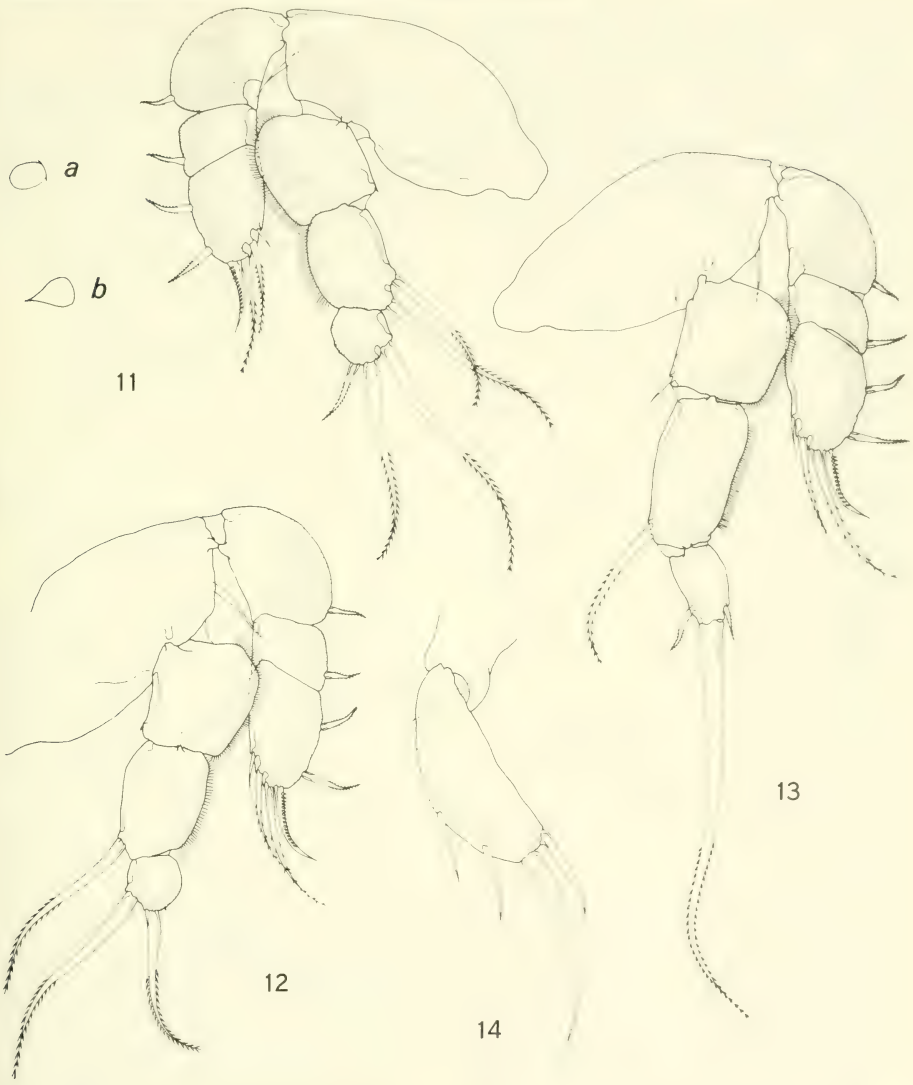


FIGURES 1-6.—*Pseudorbitacolax fimbriatus*, new species, female: 1, dorsal; 2, rostrum, ventral; 3, last abdominal segment and caudal rami, ventral; 4, same, enlarged; 5, first antenna; 6, first antenna seta.





FIGURES 7-10.—*Pseudorbitacolax fimbriatus*, new species, female (continued): 7, second antenna; 8, mandible, paragnath, first maxilla, second maxilla, labium; 9, maxilliped; 10, leg. 1.



FIGURES 11-14.—*Pseudorbitacolax fimbriatus*, new species, female (continued): 11, leg 2, a, scalelike spinules on endopod and first exopod segment, b, pointed spinules on exopod second and third segments; 12, leg 3; 13, leg 4; 14, leg 5.

segment of endopod similar to leg 2; second segment of endopod similar to leg 2 but with only one inner seta, third segment with two inner to terminal setae and one minute outer seta, outer portion of segment with scalelike spinules. Leg 4 (Figure 13) basipod, exopod, endopod first and second segments similar to leg 3 except first segment of endopod with short but well-developed inner seta; third segment of endopod with three setae (middle longest). Basal segment of leg 5 (Figure 14) with dorsal seta, terminal segment with minute spinules on outer proximal portion and four setae as indicated in the figure. Area of leg 6 obscured by egg sacs and not seen (usually present on bomolochids as three setae on genital segment).

Male.—Body form as in Figure 15. Total length 1.14 mm, greatest width 0.44 mm (measured at widest part of cephalothorax). Cephalothorax more or less rounded (length 0.41 mm) with broad rostrum. Genital segment longer than wide (247 × 177 μm) indistinctly separate from segment bearing leg 5. Abdomen 2-segmented: first segment slightly longer than wide (65 × 59 μm); second segment (59 × 88 μm) with two patches of scalelike spinules as in Figure 16. Caudal rami (Figure 16) longer than wide (50 × 35 μm), each with a single row of scalelike spinules and six setae (longest seta 531 μm).

Maxilliped (Figure 17) 4-segmented: second segment with several uneven rows of small knoblike processes, one seta, and an inner row of uniform spinules, proximal half of outer edge fringed with long hairs; last segment in form of claw with single small, toothlike process near proximal inner corner, inner edge serrate along entire length.

The single specimen examined was not dissected; therefore, detailed inspection of remaining appendages was not possible. The following description is based on gross examination of the specimen. First antenna 5-segmented with several long graceful setae and an aesthete on each of last two segments. Second antenna similar to female except spinules on third segment proportionately larger. Oral appendages similar to female. Legs 1-5 similar to *Pumiliopsis sardinellae* male with the following exceptions. Leg 2 endopod third segment with at least three setae. Leg 3 endopod third segment of *Pseudorbitacolax fimbriatus* damaged and examination not possible.

Etymology.—The specific name, *fimbriatus*, refers to the specific name of the host fish (*Sardinella fimbriata*) from which this copepod was collected.

Remarks.—The female of this species can be separated from *P. varunae* and *P. nudus* on the basis of the size and shape of the rostrum; in *P. fimbriatus* it is slightly longer than broad, and in the other two species it is broader than long. The genital segment of *P. fimbriatus* has two prominent rounded processes that are lacking in *P. varunae* and *P. nudus*. Also, the maxilliped hook of *P. fimbriatus* is much more strongly curved than in either of the other two species.

Pseudorbitacolax varunae (Bennet 1966) (Figures 18-29)

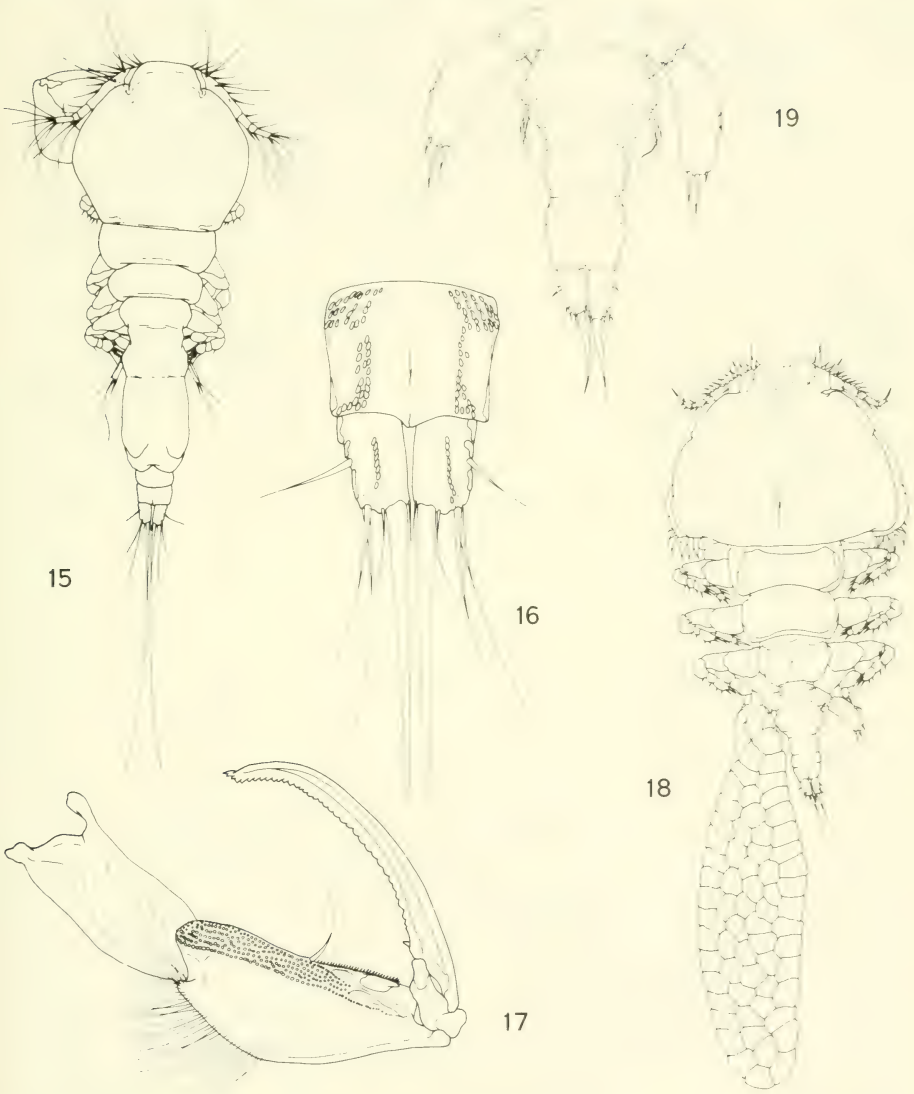
Syn: *Bomolochus varunae* Bennet 1966:295.

Material examined.—All copepods were collected from the orbit of the host fish, *Anodontostoma chacunda*: 8 ♀ from Manila, Philippine Islands; 4 ♀ from Kerala, India; 4 ♀ from Madras, India; 2 ♀ from Java; 8 ♀ from Sandakan Bay, Borneo.

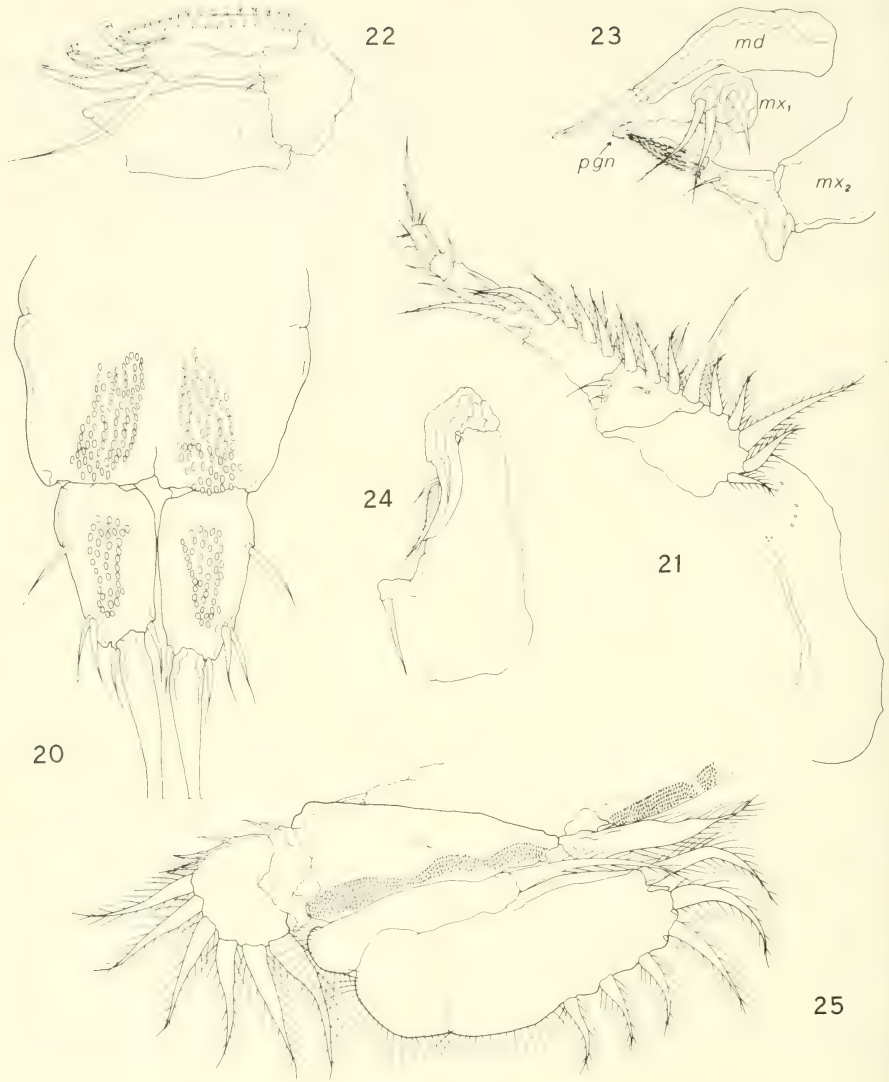
Female.—Body form as in Figure 18. Total length 2.01 mm, greatest width 1.07 mm (measured at widest part of cephalothorax); cephalothorax length 0.88 mm. Rostrum (see Figure 21) wider than long (106 × 601 μm) with no dorsal or ventral hooks. Genital segment (Figure 19) wider than long (147 × 253 μm). Abdomen (see Figure 19) 3-segmented, segmentation incomplete between second and third segments; segments measure (length × width) 88 × 153 μm, 53 × 153 μm, and 76 × 141 μm; third segment (Figure 20) with two ventral patches of scalelike spinules. Caudal rami (Figure 20) longer than wide (118 × 47 μm), each ramus with ventral patch of scalelike spinules and six setae; longest seta 165 μm.

First antenna (Figure 21) 7-segmented with an aesthete on each of the last two segments; plumose setae similar to those of *P. fimbriatus*. Second antenna (Figure 22) with 2 or 3 rows of conspicuous hooked spinules on third segment, four hooked spines and two setae distally. Mandible, paragnath, first maxilla, and second maxilla as in Figure 23; labrum with two large patches of scalelike spinules. Maxilliped (Figure 24) hook only slightly curved, with small, inner, toothlike projection.

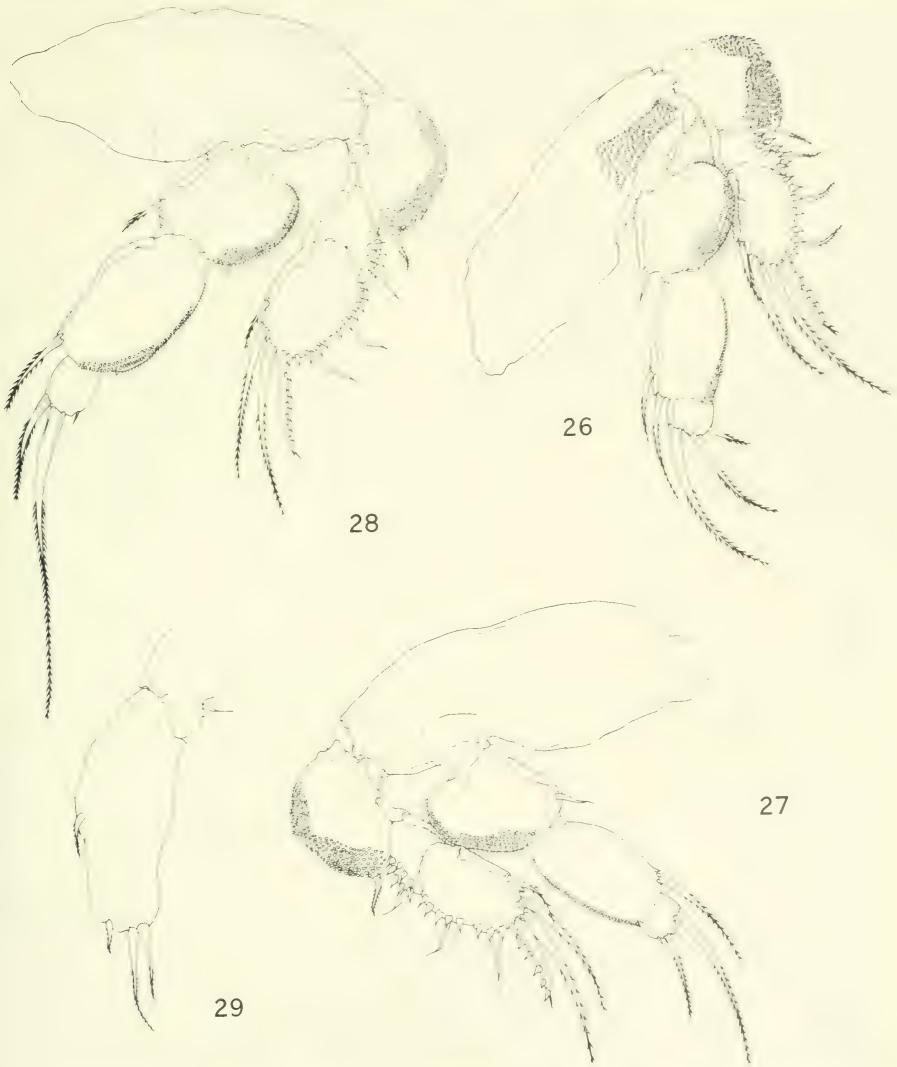
Legs 1-4 biramous, rami of legs 2-4 3-segmented. Interpodal plate of leg 1 (Figure 25)



FIGURES 15-19.—*Pseudorbitacolax fimbriatus*, new species, male: 15, dorsal; 16, last abdominal segment and caudal rami, ventral; 17, maxilliped. *Pseudorbitacolax varunae* (Bennet), female: 18, dorsal; 19, genital segment and abdomen, dorsal.



FIGURES 20-25.—*Pseudorbitacolax varunae* (Bennet), female (continued): 20, last abdominal segment and caudal rami, ventral; 21, first antenna and rostrum, ventral; 22, second antenna; 23, mandible, paragnath, first maxilla, second maxilla; 24, maxilliped; 25, leg 1.



FIGURES 26-29.—*Pseudorbitacolax varunae* (Bennet), female (continued): 26, leg 2; 27, leg 3; 28, leg 4; 29, leg 5.

with two patches of scalelike spinules; coxopod with broad, inner plumose seta and outer sclerotized spine; basipod with several rows of small, scalelike spinules above insertion of endopod; exopod 2-segmented, first segment with outer, stout, flagellated spine, second segment with three outer setiform spines and six terminal to inner plumose setae; endopod 2-segmented, first segment with inner seta, second segment with six inner to terminal setae. Basipod of leg 2 (Figure 26) with ventral patch of scalelike spinules and dorsal seta; first segment of exopod with large patch of scalelike spinules along outer half of segment and setiform spine on outer distal corner; second segment with 1 or 2 rows of stout spinules along outer edge and one outer spine, third segment with row of stout spinules along outer edge, two outer spines, one barbed terminal spine, and three inner setae; first segment of endopod with scalelike spinules along outer edge and short inner seta, second segment with scalelike spinules along outer edge and two inner setae, third segment small, with three setae (innermost longest). Leg 3 (Figure 27) similar to leg 2 with following exceptions: basipod lacks ventral patch of scalelike spinules; second segment of endopod with only one seta; outermost seta on endopod third segment reduced to a setule. Leg 4 (Figure 28) similar to leg 3 except middle seta of endopod third segment longest (about three times longer than innermost). Leg 5 (Figure 29) basal segment with dorsal seta; free segment slightly inflated with one outer seta and three terminal setae (middle seta longest); no surface ornamentation visible. Leg 6 represented by three setae at area of egg sac attachment (see Figure 19); setae reach to about middle of first abdominal segment. Egg sacs flattened in most specimens. (The egg sacs of ovigerous females of bomolochids parasitic in the orbit of their hosts are typically flattened. The egg sacs of a few specimens of this new species were more rounded.)

Male.—Unknown.

Remarks.—Our description of this species is in general agreement with Pillai's (1971) redescription with the following exceptions on specific points. We found the segmentation between the second and third abdominal segments less distinct than did Pillai. Pillai failed to mention the ornamentation on the ventral surface of the last abdominal segment and caudal rami. We found the first antenna to have one more segment than did Pillai. The last segment of the second antenna has four hooked spines and two setae rather than "5 claws and one stiff seta" as stated by Pillai. The maxilliped hook has a small but noticeable inner tooth. The basipod of leg 2 has a patch of scales not present on the basipods of legs 3 and 4. While these points are relatively minor, they aid in defining the species.

Pseudorbitacolax nudus (Cressey and Boyle 1973) (Figures 30-35)

Syn: *Orbitacolax nudus* Cressey and Boyle 1973:6.

Originally reported from *Herklotsichthys punctatus* from the Philippines. Additional collections of 4 ♀ from the same host species and locality (BM 1933.3.11:15-16, BM 1933.3.11:17-18).

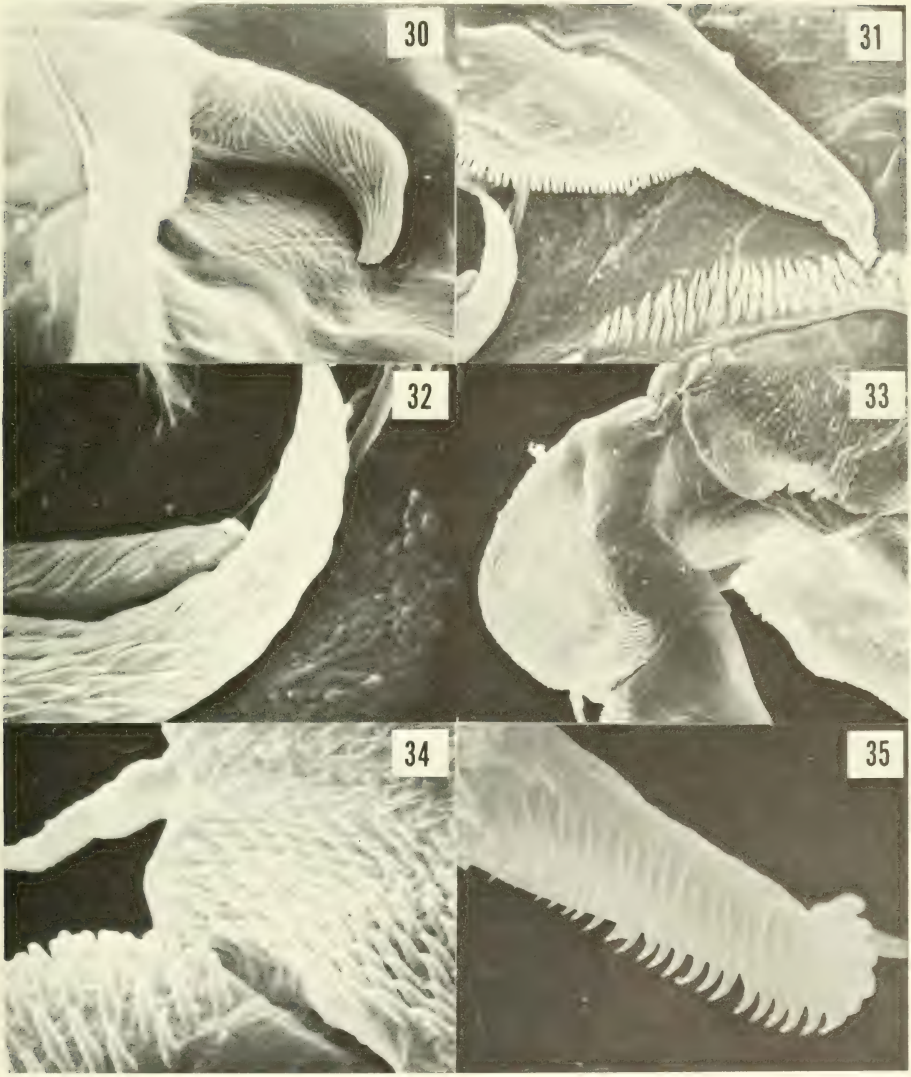
Our redescription of *Pseudorbitacolax* enabled us to reassign *Orbitacolax nudus* to this genus.

Figure 30 (SEM photo) reveals the presence of ridges on the surface of the dorsal cephalic hooks. Figure 32 shows the surface of the tip of the second maxilla to be covered with closely packed spinules. Figure 34 shows the spinules on the exopod of leg 2 to be somewhat blunted. The spinules on the terminal spines of legs 2-4 are hooklike (Figure 35) and similar to those commonly found on the second antenna.

Pumiliopsis Pillai 1967

Diagnosis.—Bomolochidae. Female: Body dorsoventrally flattened. Rostrum bilobed. Dorsal cephalic hooks present; ventral rostral hooks may or may not be present. Thoracic segments narrower than cephalothorax. Abdomen elongate, segmentation indistinct. Caudal rami each with one long, five short setae. First antenna with no modified setae. Second antenna typical of family, terminal segment with several rows of hooklets, four hooked spines, and two setae. First maxilla with three setae, middle seta more than twice the length of other two. Maxilliped hook with no outer accessory process, inner process may be present. Legs 1-4 biramous, rami 2-segmented, except endopod of leg 4 3-segmented. Leg 1 rami flattened. Last exopod segment of legs 2-4 with barbed spine.

Male.—Rostrum slightly produced. Thoracic segments each narrower than preceding segment.



FIGURES 30-35.—*Pseudorbitacolax nudus* (Cressey and Boyle), female: 30, dorsal cephalic hook (×1,475); 31, tip of mandible, paragnath, labium (×2,150); 32, tip of second maxilla (×5,000); 33, leg 2 basipod, exopod first segment (×1,000); 34, leg 2 exopod first segment, outer distal corner (×5,000); 35, leg 3 exopod third segment spine (×5,000).

Genital segment longer than broad. Abdomen 2-segmented. Caudal rami each with one very long and five short setae. First antenna extending beyond margin of cephalothorax, segments with numerous long, slender setae. Maxilliped second segment with numerous teethlike spines and large triangular process, last segment clawlike with very fine teeth at tip only. Legs 1-4 biramous, rami 3-segmented except endopod of leg 4 2-segmented. Leg 1 endopod flattened. Second endopod segment of legs 2 and 3 each with two inner setae.

Type-species.—*Pumiliopsis sardinellae* (Bennet 1964).

Remarks.—Pillai (1967) included in his generic diagnosis "rostrum triangular, longer than broad." While this is a prominent feature of the type-species, *P. sardinellae*, the shape of the rostrum of *P. plautus* is quite different. In other respects, however, *P. plautus* agrees with Pillai's description of *Pumiliopsis*. Furthermore, *Pseudorbitacolax fimbriatus* new species has a rostrum similar in shape to *Pumiliopsis sardinellae*; on the basis of several other characters, however, the two cannot be considered members of the same genus. We therefore consider the shape and relative size of the rostrum to be specific rather than generic characters.

Pumiliopsis sardinellae (Bennet 1964) (Figures 36-42)

Syn: *Pumiliopsis emarginatus* Cressey and Boyle 1973:4

Bennet originally described this copepod from the eye of *Sardinella albella* from Mandapam, South India. In 1973 we reported it from *S. perforata* (= *S. bulan*) from the Philippines. Since then we have collected the following: 12 ♀ from *S. albella* (BM 1962.3.26:96-98, BM 1963.5.6:6-7, BM 1966.11.16:28-33, BM 1966.11.16:52-54) from Mombasa, Aden, and Zanzibar; 17 ♀ 1 ♂ from *S. bulan* (BM 68.6.9:6, BM 1966.11.16:56-70, MCZ 17632, MCZ 30372, MCZ 30811, MCZ 32182) from Sarawak, Nosy Bé, Batavia, Penang, Java, and the Philippine Islands; 24 ♀ 2 ♂ from *S. fimbriata* (BM 84.5.15:27-28, BM 1965.7.5:11-13, BM 1965.7.5:15-16, BM 1966.1.28:20, BM 1966.2.28:10-11, BM 1966.11.20:2, BM 1970.4.24:1-20) from Sri Lanka, Thailand, Hong Kong, and Formosa; 4 ♀ from *S. jussieui* (BM 1973.4.5:8-9) from Thailand. All additional collections were from the eye of the host.

Since our description of *P. emarginatus* in 1973 we collected additional material from *S. albella*, Bennet's type host for *P. sardinellae*. This, along with the minor differences noted between the two copepods (segmentation of abdomen, setation of leg 3 endopod of female, segmentation of legs 1-4 of male) have led us to conclude that *P. emarginatus* is synonymous with *P. sardinellae*. The differences noted could be due to the age or condition of the specimens examined.

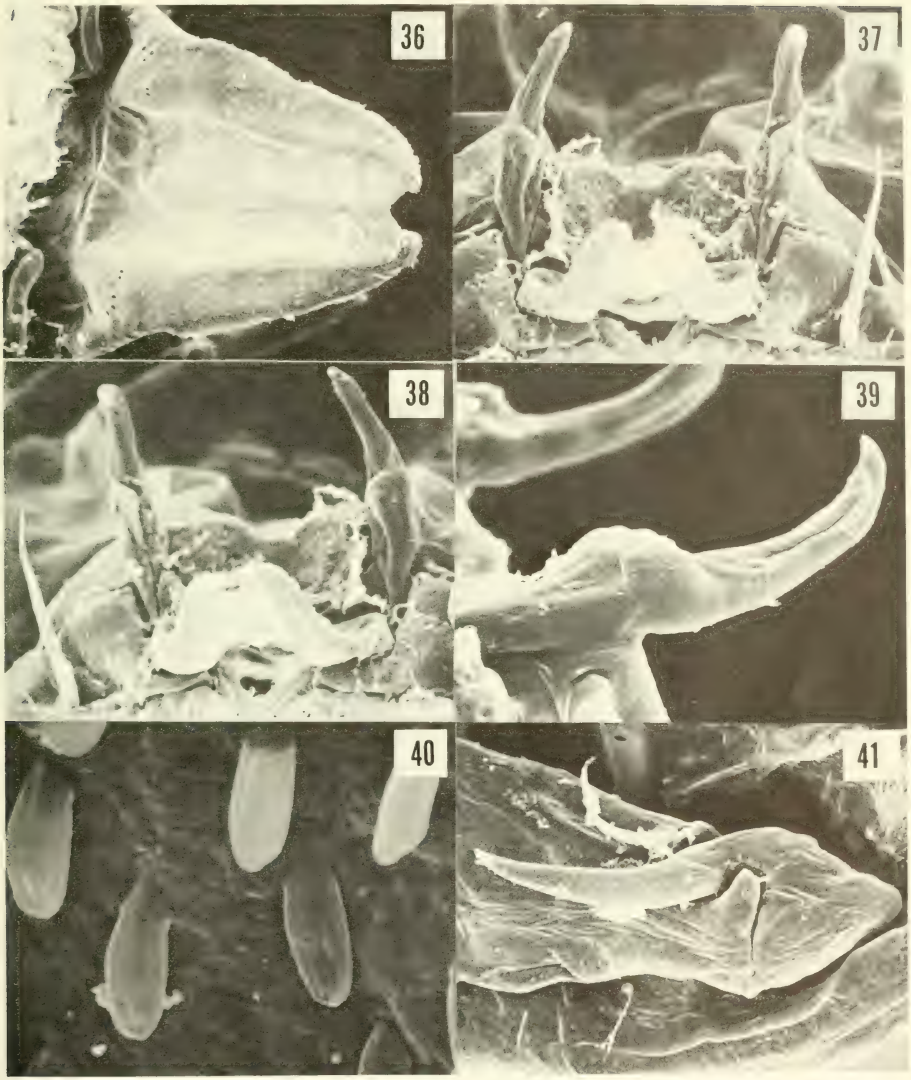
Scanning electron micrographs of the female of this species reveals features not easily seen with the light microscope. The rostrum (Figure 36) has a ventral groove with a cluster of pores near each outer basal margin. The cephalic "horns" (Figures 37-39) appear to be grooved ventrally. Figures 40 and 42 show the nature of the scales on the labrum and leg 1.

Pumiliopsis plautus Cressey and Boyle 1973 (Figures 43-46)

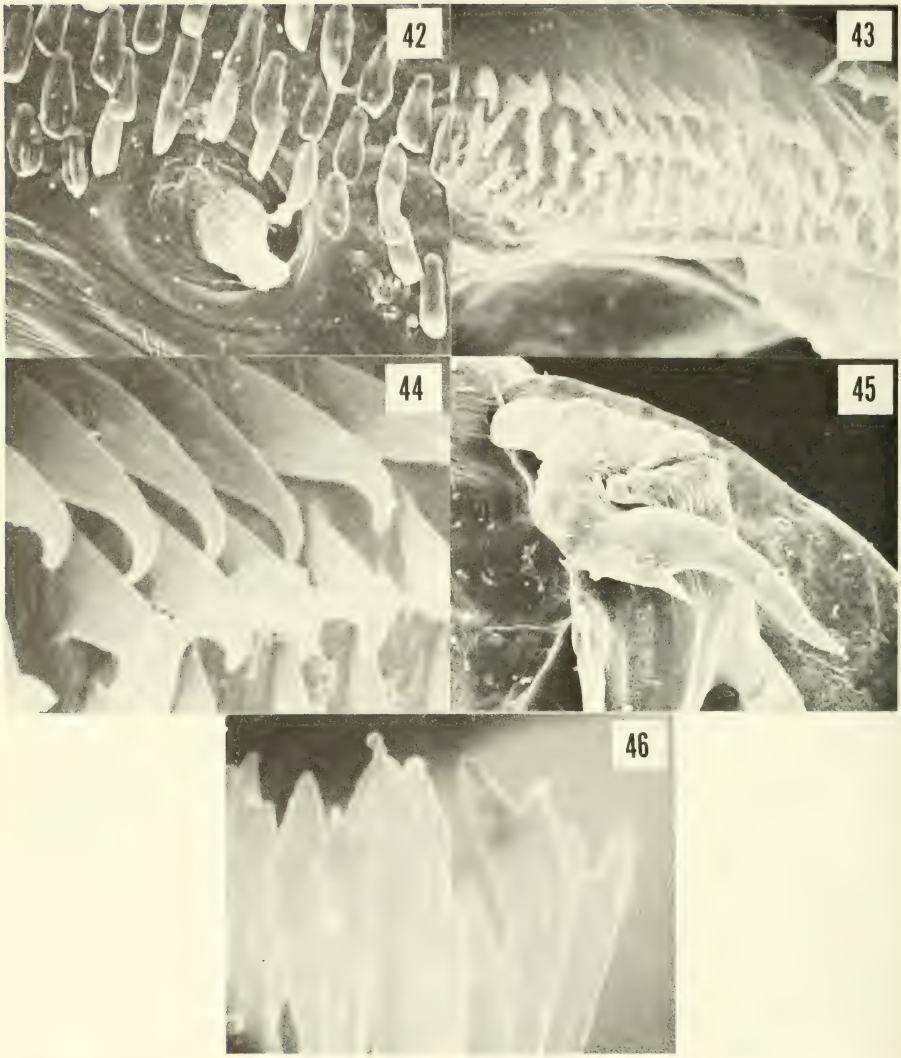
Syn: *Pumiliopsis spathepedes* Bennet 1975:156.

Originally described from *Sardinella sirm* and *S. leiogaster* (= *S. sirm*) from the Philippines. Bennet (1975) reported collecting 50 females from the eyes of *S. sirm* from Tuticorin, India. We collected an additional 6 ♀ from the same host (BM 1962.3.26:119-122, BM 1963.5.6:5, BM 1964.12.14: 180-185) from Zanzibar and Aden.

Bennet's (1975) description of *P. spathepedes* is essentially in agreement with that of *P. plautus* (1973) with the following differences. Bennet did not observe a paragnath; however, one is present. He also failed to observe the tooth on the inner margin of the maxilliped hook (this process may be difficult to detect with the specimen lying flat). The rami of leg 1 are both 2-segmented rather than 3 as stated by Bennet, and he apparently mistook the coxopod with its seta for the first endopod segment; the terminal exopod segment has three spines and six setae rather than one spine and six setae. The basipods and exopods of legs 2-4 are all similar: the basipods each have one dorsal seta and two ventral patches of spinules; the second segment of the exopods each have three stout outer spines, one apical barbed spine, and two terminal setae. The second endopod segment of leg 2 has two small outer spinules and five terminal to inner setae rather than the armature reported by Ben-



FIGURES 36-41.—*Pumiliopsis sardinellae* (Bennet), female: 36, rostrum, ventral (×500); 37, rostrum and dorsal cephalic hooks, head-on view (×260); 38, rostrum and dorsal cephalic hooks, head-on view (×260); 39, dorsal cephalic hook, lateral view (×500); 40, scales on labrum (×10,000); 41, maxilliped (×400).



FIGURES 42-46.—*Pumiliopsis sardinellae* (Bennet), female (continued): 42, scales on basipod of leg 1 (×3,500). *Pumiliopsis plautus* Cressey and Boyle, female: 43, second antenna (×1,900); 44, hooklets on second antenna (×7,000); 45, maxilliped (×500); 46, leg 4 endopod hairs (×10,000).

net. The first endopod segment of leg 3 does have a very short inner spinule. The last endopod segment of leg 4 has a small outer seta in addition to the two mentioned by Bennet. Leg 5 has a total of four setae on the terminal segment, one on the midouter margin and one subterminally in addition to the two terminal setae Bennet noted.

The scanning electron micrographs of the female indicate the hooklike nature of the ornamentation on the second antenna (Figures 43, 44) and the bifurcate tips on the lateral hairs on the endopod of leg 4 (Figure 46).

Pumiliopes Shen 1957

Diagnosis:—Bomolochidae. Female: Body dorsoventrally flattened. Rostrum only slightly produced, rounded, broader than long. Thoracic segments bearing legs 2-5 free, each segment slightly narrower than preceding one. Genital segment wider than last thoracic segment. Abdomen 3-segmented, segmentation may be indistinct. Caudal rami each with one long and five short setae. Neither dorsal cephalic nor ventral rostral hooks present. First antenna with no modified setae. Second antenna 3-segmented, last segment subdivided; subterminal portion with 1 or 2 rows of hooklets and one stout claw, terminal portion with three hooked spines and two setae. First maxilla with no or three short setae. Second segment of second maxilla produced posteriorly. Maxilliped hook with no accessory processes. Legs 1-4 biramous, rami 2-segmented except leg 4 endopod 3-segmented. Leg 1 rami flattened. Last segment of exopod of legs 2-4 with smooth, stout, clawlike spine.

Male.—Unknown.

Type-species.—*Pumiliopes opisthopteri* Shen 1957.

Remarks.—In Shen's (1957) description of *P. opisthopteri* he reported no setae on the first maxilla, and based on that report we have included it in the generic diagnosis. This condition, however, is unique in bomolochids; therefore, we consider Shen's description of the first maxilla to be tentative until additional material of this species can be examined.

Pumiliopes opisthopteri Shen 1957

Originally described from the "left eye" of *Opisthopterus tardoore* from Yin-ku Bay, Hainan Island, China. This copepod has not been reported since and we did not recover specimens in our examination of 24 specimens of the original host species (including specimens from China).

Pumiliopes jonesi (Bennet 1967)

Syn: *Bomolochus jonesi* Bennet 1967:132.
Pumiliopes capitulatus Cressey and Boyle 1973:1.

Bennet originally described this copepod as *Bomolochus jonesi* from a collection of over 200 specimens collected from under the adipose eyelids of *Rastrelliger kanagurta* (Scombridae) from Calicut, India. In 1973 we collected the same species of copepod, which we reported as *P. capitulatus*, from the orbit of *Clupanodon punctatus* (a clupeid). Our additional collections from clupeids include 1 ♀ from *C. punctatus* (BM 93.4:21-28) from Hae-yoe Chi Kiang and 3 ♀ from *Herklotsichthys displonotus* (BM 1967.11.13:1-9) from Singapore.

We also recovered 35 females from the orbits of the following scombrid fishes (all USNM collections): 17 from *R. kanagurta* from the Red Sea, Sri Lanka, Madras, India, Philippine Islands, and Java; 2 from *R. faughni* from the Philippine Islands; 13 from *Scomber japonicus* from the Gulf of Guinea, Mauritania, and Zanzibar; 3 from *S. australasicus* from the Philippine Islands. We have reported these scombrid collections in more detail in a paper describing the parasitic copepods of scombrid fishes (Cressey and Cressey 1980).

Due to the larger numbers of *P. jonesi* collected from scombrids rather than clupeids, we consider scombrids to be the preferred hosts of this copepod.

A comparison of Bennet's (1967) description of *Bomolochus jonesi* and our (Cressey and Boyle 1973) specimens and description of *Pumiliopes capitulatus* indicates that they are the same species and that Bennet's species clearly belongs in the genus *Pumiliopes*. We note the following differences in details of the two descriptions.

Bennet found only four setae on each caudal ramus; there are actually six, five apical (one long) and one lateral. Bennet reported the first antenna to be 6-segmented while we reported it to be 5-segmented, with the second segment relatively long; the exact segmentation of this appendage is often difficult to determine, but we agree on its general ornamentation. The second antenna has

one stout claw, three hooked spines, and two setae rather than five digitate claws as reported by Bennet. Bennet, like Shen in describing *P. opisthopteri*, reported no setae on the first maxilla; there are, however, three short setae present which may be difficult to detect in some specimens. The second segment of the second maxilla is produced posteriorly, a character not apparent from Bennet's figure. The exopod second segment of leg 1 has six plumose setae and three small spinules rather than seven plumose setae; the endopod second segment has six rather than four plumose setae. Bennet stated that the basipods of legs 2-4 are 2-segmented, these 2 segments are actually the coxopod and the basipod; the basipod of leg 2 has a patch of scalelike spinules near the insertion of the endopod. The second exopod segment of legs 2-4 each have small patches of spinules and weak outer spines in addition to the apical clawlike spine noted by Bennet. The "hairs" present on the outer endopod margins of legs 2-4, as noted by Bennet, are actually flattened, scalelike spinules. The free segment of leg 5 is 1-segmented, not 2-segmented, and has one lateral and three terminal setae. Leg 6 consists of three rather than two setae on the genital segment.

Pumiliopes squamosus Cressey and Boyle 1973

Originally described from *Sardinella zunasi* from Nagasaki, Japan. Additional collections include 4 ♀ from *S. fimbriata* (BM 1965.7.5:1-10) from Hong Kong; 3 ♀ from *S. fimbriata* (BM 1966.11.16:57-70) from Nosy Bé, Madagascar; 13 ♀ from *S. zunasi* (BM 1905.6.6:13-22, BM 1971.2.8:151-153) from Japan; 2 ♀ from *S. jussieui* (MCZ 30806) from Batavia. All copepods collected from the orbit of the host fish.

LITERATURE CITED

BENNET, P. S.
1964. On *Bomolochus sardinellae* sp. nov. (Copepoda, Cyclopoida) parasitic on *Sardinella albella*. J. Mar. Biol. Assoc. India 6:84-88.
1966. *Bomolochus varunae*, a new species of parasitic copepod from *Anodontostoma chacunda* (Hamilton Buchanan). J. Mar. Biol. Assoc. India 8:295-301.
1967. On *Bomolochus jonesi* sp. nov. parasitic on the eye of the Indian mackerel *Rastrelliger kanagurta*. J. Mar. Biol. Assoc. India 9:132-136.
1975. *Pumiliopsis spathepedes* sp. nov., a cyclopoid copepod parasitic on the eye of *Sardinella sirm*. J. Mar. Biol. Assoc. India 16:156-160.

CRESSEY, R. F., AND H. BOYLE.
1973. Five new bomolochid copepods parasitic on Indo-Pacific clupeid fishes. Smithson. Contrib. Zool. 161:1-25.

CRESSEY, R. F., AND H. B. CRESSEY.
1980. The parasitic copepods of mackerel and tuna-like fishes (Scombridae) of the world. Smithson. Contrib. Zool. 311:1-186.

PILLAI, N. K.
1967. Redescription of *Bomolochus sardinellae* Bennet and its transfer to *Pumiliopsis* gen. nov. (Copepoda). Crustaceana 12:249-256.
1971. On the transfer of *Bomolochus varunae* Bennet to *Pseudorbitacolax* gen. nov. (Copepoda: Bomolochidae). J. Zool. Soc. India 23:13-19.

SHEN, C.
1957. Parasitic copepods from fishes of China, Part I: Cyclopoida (1). Acta Zool. Sin. 9(4):297-327.

TEMPERATURE EFFECTS ON GROWTH AND YOLK UTILIZATION IN YELLOWTAIL FLOUNDER, *LIMANDA FERRUGINEA*, YOLK-SAC LARVAE

W. Huntting Howell[1]

ABSTRACT

Embryos and yolk-sac larvae of yellowtail flounder, *Limanda ferruginea*, were incubated at 4°, 8°, 10°, and 12° C. Embryos incubated at 8° and 10° C produced significantly larger yolk-sac larvae at hatching than those incubated at 4° and 12° C. Yolk utilization rate was positively correlated with temperature. Growth in length was fastest at 12° C. At yolk-sac absorption there was no significant difference in size among larvae incubated at 8°, 10°, or 12° C. Efficiency of yolk utilization prior to hatching was 86.2, 76.8, 73.5, and 45.9% for 12°, 10°, 8°, and 4° C. Overall yolk utilization efficiency from fertilization to yolk-sac absorption was highest at 12° C (47.1%), intermediate at 8° and 10° C (43.8 and 42.2%), and lowest at 4° C (29.8%). Efficiency decreased during the course of development at all four temperatures.

Based on the experimental results, it appears that sea temperatures between 8° and 12° C would have little, if any, differential effect on larval size at yolk-sac absorption and therefore ability to survive. It also appears that 4° C may be at or near the lower thermal limit for successful reproduction of southern New England yellowtail flounder.

The yellowtail flounder, *Limanda ferruginea*, is an important commercial species in both the New England and Canadian otter trawl fisheries. Yellowtail flounder range from the Gulf of St. Lawrence south to lower Chesapeake Bay (Bigelow and Schroeder 1953). Royce et al. (1959) and Lux (1963) found that there are five relatively distinct stocks within this range with little migration occurring between them: Georges Bank, Cape Cod, Nova Scotian, Newfoundland, and southern New England.

Over the past 35 yr, landings from the southern New England ground have fluctuated widely (Royce et al. 1959; Lux 1964, 1969; Sissenwine 1974), with a sharp decline observed in the late 1940's not accompanied by the usual symptoms of overfishing, i.e., a decline in average size, increased percentage of young fish, or increased growth rate. Royce et al., (1959) suggested the decline was caused by a warming trend inducing a temporary northeastward shift of the population center away from the southern New England grounds. Sissenwine (1974) demonstrated a significant inverse relationship between water temperature and equilibrium catch and recruitment.

The correlation between temperature and yellowtail flounder abundance is an indication that temperature may be causing fluctuations in the fishery. This research was designed to investigate the effect of temperature on growth rate, size at hatching and yolk-sac absorption, and yolk utilization rate and efficiency. Most fisheries biologists agree that early life history stages of fishes are the most vulnerable due to their small size, poor swimming ability, and susceptibility to rapid environmental changes (May 1974a). Because of this, the total set of environmental parameters in which these young fishes develop will largely determine their collective success or failure, and consequently their year-class strength. During larval development, the time when the larva changes from its endogenous source of food (yolk) to exogenous feeding is a "critical period" in the organism's life history (Hjort 1926; Marr 1956; Toetz 1966; May 1974a). Particularly important to successful initiation of exogenous feeding is the size and condition of the larva (Blaxter and Hempel 1963; Braum 1967). To a large extent size and condition will depend on the efficiency with which the organism is able to convert its yolk to larval tissue. Any environmental variable that affects conversion efficiency could affect larval size, and consequently larval ability to begin feeding. Taken over the entire population of larvae, year-class strength could be significantly affected by such environmental influences.

One such variable affecting yolk utilization efficiency is temperature (e.g., May 1974b). Because temperature has been suggested as the dominant environmental variable affecting yellowtail flounder abundance and because other in-

[1]Department of Zoology, University of Rhode Island, Kingston, R.I.; present address: Department of Zoology, University of New Hampshire, Durham, NH 03824.

Manuscript accepted February 1980.
FISHERY BULLETIN: VOL. 78, NO. 3, 1980.

vestigators have found that temperature can affect yolk utilization efficiency and thereby subsequent size and feeding ability, the current study examines the hypothesis that temperature affects yolk utilization efficiency and size of yellowtail flounder larvae.

METHODS

Adult yellowtail flounder were collected southeast of Block Island, R.I., on 28 March 1979 aboard a commercial fishing vessel. They were placed in a 680 l tank periodically supplied with running seawater and transported to the laboratory where they were held, four to a tank, in 286 l aquaria supplied with a continuous flow of filtered seawater.

To induce ripening, both sexes were anesthetized with tricaine methanesulfonate (MS-222[2]) at a concentration of 1:20,000 g and injected intramuscularly with 2.0 mg of carp pituitary dissolved in marine fish Ringer's solution per kilogram of fish wet weight following Smigielski (1979). Daily injections continued until spawning occurred. Two females of 34.4 and 42.0 cm TL (total length) were anesthetized and their eggs manually stripped into a glass bowl containing 0.45 μm filtered, ultraviolet-treated seawater (34.0‰ salinity, 10.5° C). The eggs were fertilized with milt stripped from two anesthetized males (34.5 and 33.0 cm TL). The fertilized eggs were divided volumetrically among four 6 l black plastic pans containing seawater identical to that in which fertilization had occurred. Twenty-five IU/ml penicillin and 0.02 mg/ml streptomycin were added to each pan as an antibiotic. These pans were placed in temperature-regulating circulation baths, gently aerated, and allowed to equilibrate slowly to the test temperatures. The four test temperatures chosen (4°, 8°, 10°, and 12° C) were maintained at 4.5±0.6°, 8.7±0.6°, 10.3±0.5°, and 12.2±0.6° C (mean ± 1 SD). The temperatures chosen encompass the range over which most eggs and larvae of yellowtail flounder have been collected in nature (Royce et al. 1959; Colton 1972; Smith et al. 1975). Dissolved oxygen and salinity ranged from 7.6 to 8.1 mg/l and 33.0 to 34.0‰. Photoperiod was 12D:12L throughout the experiment.

Measurements of egg and yolk diameters of a random sample of unfertilized eggs (n = 100) were made by ocular micrometer, and egg and yolk volumes calculated.

Prior to weighing, fresh unfertilized eggs were rinsed in three changes of isotonic 0.9% (weight/volume) ammonium formate to remove residual saltwater. Mean dry weight and ash-free dry weight of 390 eggs were determined to the nearest 1.0 μg, using a Perkin-Elmer electrobalance following the method of Laurence (1973). To determine the mean dry weight and ash-free dry weight of yolk per egg it was necessary to subtract mean dry and ash-free dry weight of the egg capsule (zona radiata) from the two values. Twenty-six capsules were removed from embryos just prior to hatching and dry weights and ash-free dry weights were determined by the method previously cited. Mean capsule weights were subtracted from the mean values of dry weight and ash-free dry weight of unfertilized eggs. The difference was taken as the mean dry and ash-free dry weight of yolk per egg. As both mean yolk weight and mean yolk volume were known, it was possible to calculate the dry weight and ash-free dry weight of yolk for any given volume.

Random samples of 25 yolk-sac larvae were removed from each temperature treatment beginning 2 h after hatching, and continuing at 24-h intervals until the experiments were terminated. Yolk-sac measurements were made with an ocular micrometer. The volume of the elliptical yolk sac (V_{ys} in cubic millimeters) was calculated from the formula for a spheroid:

$$V_{ys} = (\pi/6)LH^2 \quad (1)$$

where L is the length (millimeters) and H the height (millimeters) of the yolk sac (Blaxter and Hempel 1963). At each sampling period the length from tip of snout to tip of notochord was measured to the nearest 0.01 mm for each of the larvae sampled using an ocular micrometer. The fish then were rinsed in ammonium formate, and mean dry weights and ash-free dry weights determined as previously described.

Because of inherent variability in micromeasurements, data were smoothed using linear regression to relate ash-free dry weights of yolk-sac larvae and yolk-sac volumes to numbers of hours posthatch at all four temperatures. Ash-free dry weights of yolk-sac larvae and yolk-sac volumes were predicted using regression equations for each 24-h time interval and temperature. Predicted

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

yolk-sac volume (cubic millimeters) then was multiplied by the calculated ash-free dry weight of a cubic millimeter of yolk to yield the ash-free dry weight of the yolk within the yolk sac. This value was subtracted from the predicted ash-free dry weight of the yolk-sac larvae to give the ash-free dry weight of the larval tissue alone. The validity of using the same ash-free dry weight (and caloric value) of yolk throughout the yolk-sac stage has been demonstrated by Lasker (1962).

Temperature effects on yolk utilization rate were determined using analysis of covariance to compare the slopes of the regression lines. The relationship between larval notochord length and hours posthatch was nonlinear. Growth curves, linearized by logarithmic (natural) transformation of the time axis (hours posthatch), were compared by analysis of covariance. Notochord lengths, ash-free dry weights of yolk-sac larvae, and yolk-sac volumes at time of hatching and yolk-sac absorption for the four different temperatures were compared using analysis of variance. Where significant differences were found, the Student-Newman-Keuls (SNK) test was used to locate individual treatment differences.

Caloric values of yolk and larval tissue were determined by wet oxidation following Maciolek (1962). Ten samples of unfertilized ova were used to determine the caloric content of yolk. Caloric content of larval tissue was determined from finely ground samples of larvae after total yolk absorption. Three samples each were done from larvae reared at 8° and 12° C. No calorimetry was attempted at 4° and 10° C since insufficient numbers of larvae were available at yolk-sac absorption.

Yolk utilization efficiency, expressed as a percentage, is defined as the ash-free dry weight of the larva minus its yolk (or its caloric equivalent) at time t, divided by the ash-free dry weight of yolk (or its caloric equivalent) that had been used from fertilization to time t. Details of this method are described elsewhere (Toetz 1966; Laurence 1969). Because variability was high in ash-free dry weight measurements, it was not possible to calculate meaningful daily efficiencies. Thus efficiencies were calculated at ony two points in time—at hatching and at yolk-sac absorption. Efficiencies also were calculated using ash-free dry weights of larvae minus their yolk sacs and ash-free dry weights of yolk utilized, as predicted by linear regressions. These values were used to examine trends in efficiency over time.

TABLE 1.—Summary of size, ash-free dry weight (AFDW), and caloric value of unfertilized yellowtail flounder eggs.

	n	Mean	SD
Egg diameter, mm	100	0.7566	0.0079
Yolk diameter, mm	100	.7324	.0126
Egg volume, mm^3	100	.2268	.0071
Yolk volume, mm^3	100	.2059	.0105
Total AFDW, mg	390	.0127	.0009
Egg capsule AFDW, mg	26	.0006	.0001
[1]Yolk AFDW, mg	—	.0121	—
Cal/g AFDW of yolk	3	4,268.3	155.48
[1]AFDW, mg, per mm^3 yolk	—	.059	—

[1]Since the mean was derived by subtraction, no sample size or standard deviation are given.

RESULTS

Data on size, ash-free dry weight, and caloric value of unfertilized eggs from the females used in this study are given in Table 1. The mean egg diameter (0.75 mm) is slightly smaller than the mean diameters of 0.9 and 0.88 mm reported by Bigelow and Schroeder (1953) and Colton and Marak.[3]

Incubation temperature affected both the length and weight of yolk-sac larvae at time of hatching, but not at yolk-sac absorption (Table 2). At hatching, notochord length was significantly longer in larvae incubated at 8° and 10° C than in those incubated at 12° and 4° C (ANOVA, SNK, $P<0.05$). Among the four temperatures, no significant differences (ANOVA, $P>0.05$) were found between ash-free dry weights of entire yolk-sac

[3]Colton, J. B. Jr., and R. R. Marak. 1969. Guide for identifying the common planktonic fish eggs and larvae of Continental Shelf waters, Cape Sable to Block Island. U.S. Bur. Commer. Fish., Biol. Lab., Woods Hole, Mass., Lab. Ref. 69-9, 43 p.

TABLE 2.—Mean ± standard deviation of lengths, ash-free dry weights, and yolk-sac volume of yellowtail flounder reared at four temperatures. Values connected by vertical lines are not significantly different (ANOVA, SNK, $P>0.05$).

Temperature (° C)	Sample size	At hatching: Notochord length (mm) at hatching	At hatching: Yolk-sac volume (mm^3)	At hatching: Ash-free dry weight of yolk-sac larvae (mg)	At yolk-sac absorption: Ash-free dry weight of yolk-sac larvae (mg)	At yolk-sac absorption: Notochord length (mm)
4	25	2.117±0.213	0.1155±0.016	0.0086±0.001	—	—
12	50	2.096±0.126	.1213±0.020	.0116±0.002	0.0040±0.001	3.458±0.218
8	25	2.494±0.138	.0958±0.012	.0100±0.002	.0043±0.001	3.542±0.189
10	35	2.419±0.215	.0978±0.014	.0119±0.002	.0042±0.001	3.406±0.190

larvae compared at hatching. Yolk-sac volumes, however, differed significantly. Larvae reared at 12° and 4° C had significantly larger yolk volumes than those reared at 8° and 10° C (ANOVA, SNK, $P<0.05$). Larval tissue weight is taken as the difference between ash-free dry weight of the entire yolk-sac larva and ash-free dry weight of yolk. Since total ash-free dry weight was not significantly different between the four temperatures, it follows that the ash-free dry weight of the larval tissue alone must be significantly greater in those larvae reared at 8° and 10° C. This coincides with the difference seen in length. At yolk-sac absorption there were no significant differences either in length or ash-free dry weight of yolk-sac larvae (ANOVA, $P>0.05$) for the three temperatures where these variables were measured.

Notochord length increased with time after hatching (Table 3). Analysis of covariance revealed that larvae incubated at 12° C grew significantly faster than those at the other temperatures ($P<0.05$). Larvae at 4° C grew at an intermediate rate that was significantly different ($P<0.05$) from fish in other treatments. No significant difference ($P>0.05$) in growth rate was evident between 8° and 10° C larvae. Fish in both of these treatments exhibited the slowest growth rates ($P<0.05$). Regression coefficients of ash-free dry-weight of yolk-sac larvae and yolk-sac volumes vs. hours posthatch were significantly different ($P<0.001$) from zero (Table 3).

Ash-free dry weight of the larva minus its yolk sac at a particular temperature and time was calculated as the difference between the predicted total ash-free dry weight and the predicted ash-free dry weight of the yolk (Tables 4-7). Predicted values indicate that embryo weight increases linearly with time at all temperatures except 8° C (Table 5) where it remains constant.

Temperature effects on yolk utilization rate were examined by comparing the regression coefficients of the four equations for decrease in yolk-

TABLE 3.—Predictive linear equations ($Y = a + bX$) derived from least squares linear fits of the yellowtail flounder data. All equations are based on measurements taken every 24 h between hatching and yolk-sac absorption. AFDW = ash-free dry weight, and ln = natural logarithm.

Variables Y vs. X and temperature (° C)	Sample size	a	95% confidence limit for a	b	95% confidence limit for b	r
Notochord length (mm) vs. ln hours posthatch:						
4	308	1.6446	0.1192	0.27799	0.02564	0.81
8	228	2.2737	.0919	.21710	.02147	.85
10	195	2.2464	.0997	.20723	.02563	.83
12	225	1.8852	.0660	.30749	.01681	.95
AFDW yolk-sac larvae (mg) vs. hours posthatch:						
4	58	.0092	.0008	-.000021	.000005	.79
8	39	.0103	.0009	-.000035	.000008	.86
10	28	.0106	.0016	-.000046	.000016	.81
12	36	.0114	.0011	-.000047	.000010	.88
Yolk-sac volume (mm^3) vs. hours posthatch:						
4	308	.1139	.0028	-.000432	.000017	.95
8	203	.0840	.0036	-.000584	.000036	.94
10	170	.0931	.0034	-.000822	.000050	.95
12	200	.1068	.0054	-.000899	.000067	.92

TABLE 4.—Predicted values of yolk-sac larval weight, yolk-sac volume and weight, larval tissue weight, and calculated efficiencies at 4° C. AFDW = ash-free dry weight.

Hours posthatch	Yolk-sac larvae (mg AFDW)	Yolk-sac volume (mm^3)	Yolk[1] (mg AFDW)	Larval tissue[2] (mg AFDW)	Yolk utilized[3] (mg AFDW)	Efficiency[4]
2	0.0092	0.1131	0.0067	0.0025	0.0054	46.3
24	.0087	.1035	.0061	.0026	.0060	43.3
48	.0082	.0932	.0055	.0027	.0066	40.9
72	.0077	.0828	.0049	.0028	.0072	38.9
96	.0072	.0724	.0043	.0029	.0078	37.2
120	.0067	.0620	.0037	.0030	.0084	35.7
144	.0061	.0516	.0030	.0031	.0090	34.4
168	.0056	.0413	.0024	.0032	.0097	33.0
192	.0051	.0309	.0018	.0033	.0103	32.0
216	.0046	.0205	.0012	.0034	.0109	31.2
240	.0041	.0101	.0006	.0035	.0115	30.4
264	.0036	0	0	.0036	.0121	29.8
288	.0031	0	0	.0031	.0121	25.6

[1]Yolk-sac volume times 0.059.
[2]Yolk-sac larvae minus yolk.
[3]0.0121 minus yolk
[4]Larval tissue divided by yolk utilized times 100.

TABLE 5.—Predicted values of yolk-sac larval weight, yolk-sac volume, weight, and caloric value, larval tissue weight and caloric value, and calculated efficiencies at 8° C. AFDW = ash-free dry weight.

Hours posthatch	Yolk-sac larvae (mg AFDW)	Yolk-sac volume (mm^3)	Yolk[1] (mg AFDW)	Larval tissue[2] (mg AFDW)	Yolk utilized[3] (mg AFDW)	Efficiency[4]	Caloric value of yolk utilized[5]	Caloric value of larval tissue[6]	Caloric efficiency[7]
2	0.0102	0.0828	0.0049	0.0053	0.0072	73.6	0.0307	0.0167	54.4
24	.0094	.0670	.0040	0054	.0081	66.7	.0346	.0170	49.1
48	.0086	.0559	.0033	0053	.0088	60.2	.0376	.0167	44.4
72	.0078	.0419	.0025	0053	0096	55.2	.0410	.0167	40.7
96	.0069	.0279	.0016	0053	.0105	50.5	0448	.0167	37.3
120	.0061	.0138	0008	0053	0113	46.9	.0482	0167	34.6
144	.0053	0	0	0053	0121	43.8	.0516	.0167	32.4

[1]Yolk-sac volume times 0.059.
[2]Yolk-sac larvae minus yolk
[3]0.0121 minus yolk
[4]Larval tissue divided by yolk utilized times 100.
[5]Yolk utilized times 4.2683.
[6]Larval tissue times 3.6959.
[7]Caloric value of larval tissue divided by caloric value of yolk utilized times 100.

TABLE 6.—Predicted values of yolk-sac larval weight, yolk-sac volume and weight, larval tissue weight, and calculated efficiencies at 10° C. AFDW = ash-free dry weight.

Hours posthatch	Yolk-sac larvae (mg AFDW)	Yolk-sac volume (mm^3)	Yolk[1] (mg AFDW)	Larval tissue[2] (mg AFDW)	Yolk utilized[3] (mg AFDW)	Efficiency[4]
2	0.0105	0.0915	0.0054	0.0051	0.0067	76.1
24	.0095	0734	.0043	.0052	.0078	67.0
48	0084	0537	.0032	0052	0089	58.4
72	.0073	.0339	.0020	0053	.0101	52.5
96	.0062	.0142	.0008	.0054	0113	47.8
120	.0051	0	0	.0051	.0121	42.2

[1]Yolk-sac volume times 0.059.
[2]Yolk-sac larvae minus yolk.
[3]0.0121 minus yolk.
[4]Larval tissue divided by yolk utilized times 100.

TABLE 7.—Predicted values of yolk-sac larval weight, yolk-sac volume, weight, and caloric value, larval tissue weight and caloric value, and calculated efficiencies at 12° C. AFDW = ash-free dry weight.

Hours posthatch	Yolk-sac larvae (mg AFDW)	Yolk-sac volume (mm^3)	Yolk[1] (mg AFDW)	Larval tissue[2] (mg AFDW)	Yolk utilized[3] (mg AFDW)	Efficiency[4]	Caloric value of yolk utilized[5]	Caloric value of larval tissue[6]	Caloric efficiency[7]
2	0.0113	0.1050	0.0062	0.0051	0.0059	86.4	0.0252	0.0188	74.6
24	.0102	.0852	.0050	.0052	0071	73.2	.0303	.0192	63.4
48	0091	.0636	0038	0053	0083	63.9	.0354	.0196	55.4
72	0080	.0420	0025	0055	.0096	57.3	.0410	.0203	49.5
96	.0069	.0204	.0012	.0057	.0109	52.3	.0465	0211	45.4
120	.0057	0	0	.0057	.0121	47.1	.0516	0211	40.9

[1]Yolk-sac volume times 0.059
[2]Yolk-sac larvae minus yolk.
[3]0.0121 minus yolk
[4]Larval tissue divided by yolk utilized 100 times.
[5]Yolk utilized times 4.2683.
[6]Larval tissue times 3.6959.
[7]Caloric value of larval tissue divided by caloric value of yolk utilized times 100.

sac volume (Table 3). Analysis of covariance showed that the rate of decrease was related directly to temperature. All coefficients were significantly different ($P<0.05$) with yolk utilization being fastest at 12° C, followed by 10°, 8°, and finally 4° C.

Efficiency was estimated as ash-free dry weight of yolk converted into ash-free dry weight of larval tissue at all four temperatures. Overall efficiency was considered as the calculated efficiency at time of yolk-sac absorption. Values were lowest at 4° C (29.8%) intermediate at 8° and 10° C (43.8 and 42.2%), and highest at 12° C (47.1%) (Tables 4-7).

Efficiency in terms of calories of yolk converted into calories of larval tissue was calculatecd at 8° and 12° C (Tables 5 and 7). Estimates were obtained by dividing the caloric value of larval tissue at time t by the estimated caloric value of yolk utilized to time t. Calories per milligram ash-free dry weight of larval tissue at yolk-sac absorption were 3.152 ± 0.37 at 8° C and 3.696 ± 0.23 at 12° C. Analysis of variance indicated the two values were not different ($P>0.10$). Efficiencies based on caloric conversions were lower than those based on ash-free dry weight. Larvae reared at 12° C still ranked highest in overall efficiency (40.9%) with

larvae at 8° C showing a somewhat lower overall efficiency (32.4%).

Efficiencies calculated at hatching reflect the efficiency with which yolk was converted to larval tissue during embryological development. These values were consistently higher than overall efficiencies (Tables 4-7) and were similar in ranking. Based upon ash-free dry weight conversions, larvae at 12° C were most efficient (86.2%), followed by those at 10° C (76.8%), at 8° C (73.5%), and, last, at 4° C (45.9%). As for overall efficiencies, caloric efficiencies at hatching were lower than those calculated on an ash-free dry weight basis: 74.7% at 12° C and 54.3% at 8° C.

A decrease in efficiency with continuing development was noted at all four temperatures (Tables 4-7).

DISCUSSION

Mean diameter of eggs used in this study were slightly smaller than mean sizes reported by other investigators (Bigelow and Schroeder 1953; Colton and Marak footnote 3). Many variables can effect egg diameter. Laurence (1969) and Alderdice and Forrester (1974) have demonstrated a relationship between egg diameter and parental size. Egg diameter has also been related to incubation temperature and salinity, as well as time from fertilization (Alderdice and Forrester 1974; Alderdice et al. 1979). In addition, Blaxter and Hempel (1963) found differences in egg diameter between stocks of herring. If any of these variables affect egg size in yellowtail flounder, it appears likely that the results found here may not be comparable with reported values.

Larvae incubated at the intermediate temperatures (8° and 10° C) were significantly larger at hatching than those incubated at the extremes (4° and 12° C). This conflicts with data of Smigielski[4] who found that mean length at hatching was independent of temperature over a 6°-14° C range. One reason for the different findings may be the time at which measurements were taken. Since hatching occurs over a period of about 12-36 h, depending on the temperature, and since growth is rapid, the mean size estimated will depend on the time measurements were taken. Furthermore, Alderdice and Forrester (1974) and Alderdice and Velsen (1971) have shown that larval size at hatching can be different among fish in the same treatment depending on hatching time.

The implications of larval size at hatching may not be great relative to size at yolk-sac absorption. Upon hatching there is no need for larvae to feed actively due to their endogenous yolk supply. Because larger size confers an advantage in swimming ability, which in turn affects feeding ability (Hunter 1972), it follows that the size attained at yolk-sac absorption, when the larvae change to exogenous feeding, is more critical than the size at hatching. Analysis of growth rates from hatching to yolk-sac absorption indicate that larvae at 12° C grew significantly faster than those at other temperatures. Because of this, 12° C larvae attained a size equal to that of 8° and 10° C larvae by yolk-sac absorption. Because of the similarity in size of larvae reared at these three temperatures, it is presumed that they would be equally successful in capturing prey. Although no data were available for 4° C larvae at yolk-sac absorption, their smaller size at hatching, combined with their low conversion efficiency, should result in their being significantly smaller at yolk-sac absorption. The added fact that all larvae in the 4° C treatment died shortly before yolk-sac absorption makes it probable that 4° C is at, or near, the lower temperature limit for successful reproduction in the southern New England yellowtail flounder stock.

Yolk utilization rate, measured by decrease in yolk-sac volume over time, also was affected significantly by temperature; the higher the temperature, the more rapidly yolk was used. This is to be expected since rate of yolk (food) consumption, is one measure of the rate of physiological functions (metabolism and growth) which are temperature-dependent in most ectotherms (Brett 1970). A number of previous studies have shown similar results (e.g., Blaxter 1956; Ryland and Nichols 1967; Fluchter and Pandian 1968).

Calculated efficiencies indicate the number of calories incorporated, or the amount of yolk converted into larval tissue in a particular time interval. The remaining calories, or weight, are lost through the metabolic processes of yolk transformation, maintenance, activity, and excretion. Incubation temperatures in this study were observed to affect both rate of growth and rate of yolk utilization. Since the calculated efficiency will depend on the relationship between these two rates, a change in either rate, relative to the other, will be reflected in a change in efficiency. Because temperature affects both these rates, it is not surpris-

[4]Alphonse Smigielski, Fisheries Biologist, National Marine Fisheries Service, NOAA, Narragansett, RI 02882, pers. commun. November 1979.

ing that several investigators have found a relationship between incubation temperature and yolk utilization efficiency. Laurence (1973) found that overall efficiencies for tautog, *Tautoga onitis*, were 36.3, 25.5, and 25.8% for 16°, 19°, and 22° C. Ryland and Nichols (1967) found that for plaice, *Pleuronectes platessa*, efficiencies were roughly 35-40% at lower temperatures (2.5°-5.0° C) and 43-57% at higher temperatures (6.5°-8.5° C). Working with the Atlantic salmon, *Salmo salar*, Hayes and Pelluet (1945) found that efficiency was low (42%) at temperatures of 0°-5° C, and increased linearly with increasing temperature to 60% at 16° C.

The overall efficiencies in this study, based upon ash-free dry weights, were 43.8, 42.2, and 47.1% for 8°, 10°, and 12° C. The similarity of these values is an indication that within this temperature range, mechanisms are available whereby the increased metabolic demands of the larval tissue, caused by the higher temperatures, are balanced by an increased transfer of energy from the yolk for the building of tissues. The fact that increasing growth rate with temperature is accompanied by an increased rate of yolk utilization lends support to this hypothesis. Blaxter and Hempel (1966) also point out that overall efficiencies can be similar at different temperatures if the interrelationship between rate of rise in metabolic requirements and reduction in development time are balanced over a temperature range. Wood (1932) reported that yolk utilization efficiency in trout was independent of temperature between 7° and 12° C. Marr (1966), however, after recalculating the data, concluded that efficiency was actually higher at 10° C. Johns and Howell (1980) found that efficiencies were similar in summer flounder, *Paralichthys dentatus*, larvae at 16° and 21° C. They noted that the ratio of yolk needed for metabolism to yolk converted to tissue remained constant at the two temperatures, causing efficiencies to be similar. Although none of the investigations on yolk utilization efficiency demonstrates temperature independence, several of the studies show, over a particular section of the temperature range tested, that efficiencies are quite similar. These include work on *S. salar* (Hayes and Pelluet 1945), *Clupea harengus* (Blaxter and Hempel 1966), and *T. onitis* (Laurence 1973).

Larvae incubated at 4° C did not survive to yolk-sac absorption; however, 288 h after hatching, when approximately 2% of the yolk remained, the calculated efficiency was 25.6%. This low value indicates that the energy within the yolk was being largely used for metabolic demands other than growth of larval tissue. The relatively low efficiency of yolk conversion at 4° C adds further support to the conclusion that 4° C is a suboptimal temperature for this stock of yellowtail flounder.

A reduction in efficiency as development proceeded was noted at all four temperatures. Blaxter and Hempel (1966) noted such a decrease in herring larvae and concluded that the reduction was due to the relatively higher metabolic demands of heavier larvae. Although no metabolic measurements were made in this study, it is suspected that the explanation offered by Blaxter and Hempel (1966) applies to these results.

The hypothesis that a deficit in food energy can be caused by yolk exhaustion prior to initiation of exogenous feeding has received considerable attention. Such a deficit has been demonstrated by Lasker (1962) for the Pacific sardine, *Sardinops caerulea*. Laurence (1969, 1973) working with largemouth bass, *Micropterus salmoides*, and tautog found that no such deficit occurred in either species. Yellowtail flounder larvae reared at 8°, 10°, and 12° C in this study, as well as those reared by Smigielski (1979), all possessed darkly pigmented eyes, a functional mouth and jaw apparatus, and a completely formed gut at yolk-sac absorption. These morphological traits strongly indicate that larvae were able to begin feeding at this time. Smigielski (1979) further noted that yellowtail flounder larvae were capable of surviving for several days without food after the yolk reserves were depleted. The larva's apparent capacity to feed at yolk-sac absorption, and its ability to survive temporarily without exogenous food make it unlikely that an energy deficit significantly effects survival. This observation, combined with the fact that larvae reared at 8°, 10°, and 12° C were equal in size at yolk-sac absorption, thus conferring equal feeding and predator avoidance abilities, is an indication that larvae growing at these temperatures would have equal survival potential.

Results of this study indicate that yellowtail flounder eggs and yolk-sac larvae are eurythermal. Smith et al. (1978), studying diel vertical migrations of yellowtail flounder larvae, found that those less than about 4 mm long migrated only short distances, and thus experienced little temperature change. Larger larvae, however, were subjected to as much as a 10° C change (from 5° to

15° C) during the course of their migration, and Smith et al. concluded that yellowtail flounder larvae were "physiologically adapted to wide ranges in temperature." Even though larger yellowtail flounder larvae are apparently rather eurythermal, the fact that their zone of tolerance can be exceeded in nature is demonstrated by the observation of Colton (1959). Colton found many dead yellowtail flounder larvae across a 16 km (10-mi) transect in which the temperature rose from 8° to 20° C in <24 h. This observation does not, however, refute eurythermality in this species since the temperature changes were so extensive and abrupt.

These experimental results indicate that temperatures between 8° and 12° C have little direct effect on survival of yellowtail flounder larvae. This, combined with the observations of Smith et al. (1978) indicate that early stages of yellowtail flounder are eurythermal. Because of this, it seems doubtful if temperature causes the observed fluctuations through direct physiological means. Obviously abrupt thermal changes such as those observed by Colton (1959) could cause mass mortality and therefore poor recruitment of a year class. Perhaps it is through such a mechanism that temperature affects abundance. It is also possible that temperatures tested in this study were not high enough to demonstrate a clear relationship between a high temperature and some physiological response that would affect the larva's ability to survive.

ACKNOWLEDGMENTS

I am grateful to Tom Dykstra and the crew of the FV *Freisland* for their considerable help with collection of specimens. Al Smigielski, Mike Johns, and Gary Davis provided valuable discussions. I am also indebted to Saul B. Saila, William H. Krueger, H. Perry Jeffries, and the two anonymous reviewers who critically reviewed the manuscript and offered many helpful suggestions.

LITERATURE CITED

ALDERDICE, D. F., AND C. R. FORRESTER.
1974. Early development and distribution of the flathead sole (*Hippoglossoides elassodon*). J. Fish. Res. Board Can. 31:1899-1918.

ALDERDICE, D. F., H. ROSENTHAL, AND F. P. J. VELSEN.
1979. Influence of salinity and cadmium on the volume of Pacific herring eggs. Helgol. wiss. Meeresunters. 32: 163-178.

ALDERDICE, D. F., AND F. P. J. VELSEN.
1971. Some effects of salinity and temperature on early development of Pacific herring (*Clupea pallasi*). J. Fish. Res. Board Can. 28:1545-1562.

BIGELOW, H. B., AND W. C. SCHROEDER.
1953. Fishes of the Gulf of Maine. U.S. Fish Wildl. Serv., Fish. Bull. 53, 577 p.

BLAXTER, J. H. S.
1956. Herring rearing. II. The effect of temperature and other factors on development. Scott. Home Dep. Mar. Res. 5, 19 p.

BLAXTER, J. H. S., AND G. HEMPEL.
1963. The influence of egg size on herring larvae (*Clupea harengus* L.). J. Cons. 28:211-240.
1966. Utilization of yolk by herring larvae. J. Mar. Biol. Assoc. U.K. 46:219-234.

BRAUM, E.
1967. The survival of fish larvae in reference to their feeding behavior and their food supply. *In* S. D. Gerking (editor), The biological basis of freshwater fish production, p. 113-131. Wiley, N.Y.

BRETT, J. R.
1970. Temperature-Fishes. *In* O. Kinne (editor), Marine ecology, Vol. 1, Part 1, p. 515-560. Wiley, N.Y.

COLTON, J. B., JR.
1959. A field observation of mortality of marine fish larvae due to warming. Limnol. Oceanogr. 4:219-222.
1972. Temperature trends and the distribution of groundfish in continental shelf waters, Nova Scotia to Long Island. Fish. Bull., U.S. 70:637-657.

FLUCHTER, J., AND T. J. PANDIAN.
1968. Rate and efficiency of yolk utilization in developing eggs of the sole *Solea solea*. Helgol. wiss. Meeresunters. 18:53-60.

HAYES, F. R., AND D. PELLUET.
1945. The effect of temperature on the growth and efficiency of yolk conversion in the salmon embryo. Can. J. Res. Sect. D, 23:7-15.

HJORT, J.
1926. Fluctuations in the year classes of important food fishes. J. Cons. 1:5-38.

HUNTER, J. R.
1972. Swimming and feeding behavior of larval anchovy, *Engraulis mordax*. Fish. Bull., U.S. 70:821-838.

JOHNS, D. M., AND W. H. HOWELL.
1980. Yolk utilization in summer flounder (*Paralichthys dentatus*) embryos and larvae reared at two temperatures. Mar. Ecol. Prog. Ser. 2:1-8.

LASKER, R.
1962. Efficiency and rate of yolk utilization by developing embryos and larvae of the Pacific sardine, *Sardinops caerulea* (Girard). J. Fish. Res. Board Can. 19:867-875.

LAURENCE, G. C.
1969. The energy expenditure of largemouth bass larvae, *Micropterus salmoides*, during yolk absorption. Trans. Am. Fish. Soc. 98:398-405.
1973. Influence of temperature on energy utilization of embryonic and prolarval tautog, *Tautoga onitis*. J. Fish. Res. Board Can. 30:435-442.

LUX, F. E.
1963. Identification of New England yellowtail flounder groups. U.S. Fish Wildl. Serv., Fish. Bull. 63:1-10.
1964. Landings, fishing effort, and apparent abundance in

the yellowtail flounder fishery. Int. Comm. Northwest Atl. Fish., Res. Bull 1:5-21.

1969. Landings per unit effort, age composition, and total mortality of yellowtail flounder, *Limanda ferruginea*, (Storer), off New England. Int. Comm. Northwest Atl. Fish., Res. Bull. 6:47-52.

MACIOLEK, J. A.

1962. Limnological organic analyses by quantitative dichromate oxidation. U.S. Fish Wildl. Serv., Bur. Sport Fish Wildl., Res. Rep. 60, 61 p.

MARR, D. H. A.

1956. The 'critical period' in the early life history of marine fishes. J. Cons. 21:160-170.

1966. Influence of temperature on the efficiency of growth of salmonid embryos. Nature (Lond.) 212:957-959.

MAY, R. C.

1974a. Larval mortality in marine fishes and the critical period concept. *In* J. H. S. Blaxter (editor), The early life history of fish, p. 3-19. Springer-Verlag, N.Y.

1974b. Effects of temperature and salinity on yolk utilization in *Bairdiella icistia* (Jordan and Gilbert) (Pisces:Sciaenidae). J. Exp. Mar. Biol. Ecol. 16:213-225.

ROYCE, W. F., R. J. BULLER, AND E. O. PREMETZ.

1959. Decline of the yellowtail flounder *Limanda ferruginea* off New England. U.S. Fish Wildl. Serv., Fish. Bull. 59:169-267.

RYLAND, J. S., AND J. H. NICHOLS.

1967. Effect of temperature on the efficiency of growth of plaice prolarvae. Nature (Lond.) 214:529-530.

SISSENWINE, M. P.

1974. Variability in recruitment and equilibrium catch of the Southern New England yellowtail flounder fishery. J. Cons. 36:15-26.

SMIGIELSKI, A. S.

1979. Induced spawning and larval rearing of the yellowtail flounder, *Limanda ferruginea*. Fish. Bull., U.S. 76:931-936.

SMITH, W. G., J. D. SIBUNKA, AND A. WELLS.

1975. Seasonal distributions of larval flatfishes (Pleuronectiformes) on the continental shelf betwen Cape Cod, Massachusetts, and Cape Lookout, North Carolina, 1965-66. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-691, 68 p.

1978. Diel movements of larval yellowtail flounder *Limanda ferruginea*, determined from discrete depth sampling. Fish. Bull., U.S. 76:167-178.

TOETZ, D. W.

1966. The changes from endogenous to exogenous sources of energy in bluegill sunfish larvae. Invest. Indiana Lakes Streams 1:115-146.

WOOD, A. H.

1932. The effect of temperature on the growth and respiration of fish embryos (*Salmo fario*). J. Exp. Biol. 9:271-276.

OXYGEN CONSUMPTION AND HEMOLYMPH OSMOLALITY OF BROWN SHRIMP, *PENAEUS AZTECUS*

JAMES M. BISHOP,[1] JAMES G. GOSSELINK,[2] AND JAMES H. STONE[2]

ABSTRACT

Oxygen consumption and (or) osmoregulation of brown shrimp was measured under conditions applicable to their natural environment or culture. Shrimp were acclimated to test salinity and temperature a minimum of 1 week prior to any test and to the respirometer chamber for 1 hour prior to recording data. Time of day, effects of white-light illumination, and crowding were not found to influence significantly their mass (m) specific oxygen consumption rate (mg O_2 · g wet m^{-1} · h^{-1}); however, disturbed shrimp consumed oxygen nearly four times faster than shrimp at rest (0.56 vs. 0.13 mg O_2 · g wet m^{-1} · h^{-1}). The effects of size (3.7 and 6.7 g shrimp), salinity (10, 20, and 30‰), and temperature (18°, 23°, 28°, 33° C) on shrimp hemolymph concentrations and oxygen consumption rates showed that hemolymph osmolalities increased significantly with salinity and that oxygen consumption rates increased significantly with temperature. Mean hemolymph concentrations in 10, 20, and 30‰ salinity were 616, 696, and 774 milliosmoles, but differences among oxygen consumption rates in these salinities were negligible, supporting the hypothesis that relatively little energy is required for osmoregulation by euryhaline species. Mean hemolymph concentrations were significantly higher for 3.7 g shrimp (796 milliosmoles) than for 6.7 g shrimp (753 milliosmoles) only 30‰ salinity, indicating that the larger shrimp may be better hypoosmoregulators. At 18° C, oxygen consumption rates averaged 0.29 mg O_2 · g wet m^{-1} · h^{-1} and increased significantly at each test temperature to 0.55 mg O_2 · g wet m^{-1} · h^{-1} at 33° C. Indirect calorimetry calculations showed that juvenile shrimp (~5.2 g) in 10-30‰ salinity and 23°-28° C respired a daily equivalent approximating 3.4% of their energy content, that is, 105 calories.

Shrimp comprise the basis for the nation's most valuable seafood industry (Roedel 1973). Demand has surpassed domestic production, and in 1975 the United States imported about 37% of its annual consumption (National Marine Fisheries Service 1978). Demand and high pound value have made shrimp an attractive species for culture (Rose et al. 1975). Although shrimp (*Penaeus* spp.) culture is biologically possible, no operations have been economically successful in the United States. Reasons for this, in part, are that in spite of years of study, many basic aspects of shrimp behavior, biology, and physiology remain unknown. Fundamental to intensive husbandry of any animal is knowledge of its energy budget, i.e., its consumption and utilization of energy under specified conditions.

Energy budgets are usually depicted as flow schemes and diagrammatically trace energy derived from food to expenditures in various physiological processes (see Brody 1945; Harris 1966; Crampton and Harris 1969; Brett 1970). The amount of energy channelled through an organism and the compartmentalization of that energy depends upon environmental and physiological variables such as season, temperature, photoperiod, salinity, sex, size, age, food, crowding, stage of molt cycle, etc. (Zeuthen 1947; Waterman 1960; Prosser and Brown 1961; Crampton and Harris 1969; Brett 1970). Because metabolic demands of maintenance and feeding activity must be satisfied before growth can occur, knowledge of these demands under various conditions may be used advantageously to control or manipulate food conversion (Brett 1970). Most assimilated energy is expended in basal metabolism and maintenance (Brody 1945).

Internal respiration or intermediary metabolism is the sum of enzymatic reactions in which energy is made available for biological work (Prosser and Brown 1961), and the best measure of metabolism is caloric output (Fry 1957). Obtaining the caloric output for an experimental organism requires the determination of its oxygen consumption, carbon dioxide production, nitrogen excretion, and the caloric content of excreta (Fry

[1]Marine Resources Research Institute, South Carolina Wildlife and Marine Resources Department, P.O. Box 12559, Charleston, SC 29412.
[2]Center for Wetland Resources, Louisiana State University, Baton Rouge, LA 70803.

Manuscript accepted March 1980.
FISHERY BULLETIN: VOL. 78, NO. 3, 1980.

1957). This difficult task has seldom been carried out completely and usually oxygen consumption alone is used to measure metabolism (Fry 1957).

To date, few researchers have studied any portion of the energy budget of penaeid shrimp. The most complete attempt was that of Qasim and Easterson (1974), who ascertained energy ingested, assimilated, and egested by *Metapenaeus monoceros*. Condrey et al. (1972) tested conversion efficiencies of selected diets of *P. aztecus* and *P. setiferus*, and Nose (1964) obtained protein digestibility for *P. japonicus*. Finally, assimilation efficiencies of *P. aztecus* feeding naturally were determined by Jones (1973).

A number of investigators have studied penaeid oxygen consumption (Rao 1958; Egusa 1961; Kader 1962; Subrahmanyam 1962, 1976; Zein-Eldin and Klima 1965; Weerasinghe and Arudpragasam 1967; Steed and Copeland 1967; Kutty 1969; Ikeda 1970; Kutty et al. 1971; Venkataramiah et al. 1975, see footnote 3; Green et al. 1976; Venkataramiah et al.[4]). Subrahmanyam (1962) has shown that one shrimp, *P. indicus*, is an oxygen conformer and that its oxygen-consumption rate depends upon the partial pressure of oxygen, even at saturation levels. Thus, as the ambient oxygen concentration in a closed chamber decreases from respiration, the shrimp's respiratory rate will also decrease. Because all previous investigators, except Egusa (1961), Subrahmanyam (1976), and Venkataramiah et al. (footnote 4) used static situations to measure oxygen consumption of shrimp, their results may not be representative of respiratory rates in natural or culture conditions.

Shrimp of the genus *Penaeus* in the Gulf of Mexico exhibit a complex life cycle that includes a distinct migration between deep offshore waters and shallow estuarine waters. Shrimp enter estuaries as postlarvae and may grow from an initial size of 12 mm to lengths >100 mm before returning offshore (Williams 1965; Pérez Farfante 1969). In estuaries, shrimp experience daily and seasonal changes in salinity and temperature and, prior to emigration, are one of the most abundant and important macroinvertebrates. In this paper we report the effects of selected environmental factors influencing the shrimp's metabolic rate and (or) osmoregulation. We also estimate energy budgets for animals under typical environmental conditions. Experimental conditions were selected to be applicable to the shrimp's natural environment, i.e., typical estuarine salinities and temperatures (St. Amant et al. 1966), or to provide knowledge relevant to their intensive culture.

METHODS

Experimental Procedure

Brown shrimp, *Penaeus aztecus* Ives, were captured in a 4.9 m otter trawl in Airplane Lake, Jefferson Parish, La., between 1 September 1973 and 30 June 1974 (from November 1973 to January 1974, some pink shrimp, *P. duorarum*, may have been included among the test animals). After capture shrimp were selected for size and transported to Louisiana State University (LSU) in Baton Rouge. One of two size classes, 3.7±0.6 g (73-82 mm total length, TL) and 6.7±0.9 g (90-100 mm TL), of shrimp were used in all tests. The 3.7 g shrimp are typical of estuarine shrimp populations (St. Amant et al. 1966), and 6.7 g shrimp are frequently among the size range emigrating from estuaries (Parker 1970).

In the laboratory, shrimp were placed in polyethylene holding tanks and acclimated to test salinity and temperature combinations for a minimum of 1 wk (Sick et al. 1973) prior to any experiment. Acclimation and test temperatures were maintained to within ±1.5° C. Salinity was maintained to within ±1.5‰ (refractometer readings) with artificial sea salt. Photoperiod was kept at 12 h light, 12 h dark (12:12 LD); the photophase began at 0630 and ended at 1830 h central standard time (c.s.t.). Shrimp were starved 24 h before testing but otherwise fed daily an excess amount of an extruded pellet (FST 21-5/72A).[5] Uneaten food was removed daily. Chopped fresh shrimp or Tetra Werke's TetraMin[6] was occasionally included in the diet.

[3] Venkataramiah, A., G. J. Lakshmi, and G. Gunter. 1974. Studies on the effects of salinity and temperature on the commercial shrimp, *Penaeus aztecus* Ives, with special regard to survival limits, growth, oxygen consumption, and ionic regulation. U.S. Army Engineer WES, Vicksburg, Miss., Contract No. DACW 39-71-C-008, 134 p.

[4] Venkataramiah, A., G. J. Lakshmi, P. Biesiot, J. D. Valleau, and G. Gunter. 1977. Studies on the time course of salinity and temperature adaptation in the commercial brown shrimp *Penaeus aztecus* Ives. U.S. Army Engineer WES, Vicksburg, Miss., Contract No. DACW 39-73-C-0115, 370 p.

[5] Obtained from S. P. Meyers, Professor, Department of Food Science and Technology, Louisiana State University, Baton Rouge, LA 70803.

[6] Reference to trade names does not imply endorsement of that product by the National Marine Fisheries Service, NOAA.

A closed, continuously flowing, differential respirometer was used to measure the oxygen consumption rates. Its basic design was modified from the apparatus employed by Keys (1930) and consisted of a test chamber positioned between two oxygen polarographs through which a known volume of water flowed from a supply to a catchment reservoir (Bishop 1976). Hourly flow rates varied between 1.934 and 2.519 l depending on salinity-temperature combinations.

Prior to a test, polarograph readings were checked for identical response, shrimp were placed in the chamber, the chamber voided of air and sealed, and the water switched to flow through the test chamber. At the end of a test, water flow was again shunted past the chamber, and probe readings were rechecked to ensure similar readings. Probes were read to the nearest 0.05 ppm. If probe drift occurred and exceeded 0.15 ppm the test was discontinued and disregarded. If drift occurred, but was <0.15 ppm, it was assumed to have occurred at a constant rate, and data were corrected accordingly. After a test the shrimp were measured, sexed, and weighed individually. Except for diurnal experiments, all tests lasted 2 h. Mean live mass (m) of test shrimp is used to denote the size class of shrimp being discussed. Hourly rates of oxygen consumption are expressed on a per gram live mass basis, i.e., mg $O_2 \cdot g$ wet $m^{-1} \cdot h^{-1}$. Statistical designs and arrangements were from Cochran and Cox (1957) and Steel and Torrie (1960), and significant differences were tested at $\alpha = 0.05$ or 0.01.

Experiments

Diurnal Effects

Five 6.7 g shrimp were tested individually for 24 h under a 12:12 LD photoperiod. Test salinity and temperature was 20‰ and 25° C, respectively. Shrimp were allowed to acclimate to the test chamber during the first 1.5 h. Except for the initial 1.5 h and 1 h following each probe check, oxygen consumption data were averaged for each 15-min period and grouped into eight 3-h intervals (0630-0930, 0930-1230, ..., 0330-0630 h). An analysis of variance (ANOVA) employing a randomized block design was computed on the average oxygen consumption for each shrimp (block) during the eight 3-h intervals (treatments).

Light; Reduced-Light Effects

Four 6.7 g shrimp were individually tested while exposed to laboratory light (193 lm m^{-2}). Test salinity and temperature were 20‰ and 25° C, and tests lasted 2 h. An inverted, bottomless, opaque plastic bucket was placed over the test chamber to preclude visual disturbances. The next day each shrimp was again tested in the same sequence, but the light was reduced (<10 lm m^{-2}) by placing an intact plastic bucket over the test chamber. Two days of similar tests were repeated with three different 6.7 g shrimp except that the shrimp were first tested in reduced light. An ANOVA in a crossover design was computed on the average oxygen consumption rates of the last two 15-min periods.

Disturbance Effects

Four 6.7 g shrimp were tested singly for oxygen consumption after disturbance. Test salinity and temperature were 20‰ and 25° C, and ambient oxygen concentration was 7.4 ppm. Shrimp were placed in the test chamber, and the chamber was shaken by hand for approximately 5 min. The highest oxygen consumption rate during the following 15 min was considered to approach that for active shrimp.

The lowest oxygen consumption rate of shrimp from four randomly selected diurnal experiments was obtained to estimate standard respiration. Because both disturbance and diurnal tests were conducted at the same salinity and temperature, oxygen consumption differences between these two test conditions should result primarily from increased metabolic activity. We used t-tests comparing two sample means to test for significant differences between the shrimp's resting and active oxygen consumption rates.

Crowding Effects

The effects of crowding on the oxygen consumption of 3.7 and 6.7 g shrimp were investigated. Area of the test-chamber floor was 103.9 cm^2, and chamber volume was 240 ml. Shrimp were tested at 20‰ S (salinity) and 25° C. Light was reduced to <10 lm m^{-2} during the tests by placing an inverted, opaque plastic bucket over the test chamber. Eight replicates were obtained for 3.7 g shrimp tested in groups of one and two, and a t-test involving two sample means was employed to test for significant differences. Eight replicates of 6.7 g

shrimp in groups of one, two, and three, and four replicates of 6.7 g shrimp in groups of four were also tested. An ANOVA in a completely randomized design was computed for the average oxygen consumption of the last two 15-min periods of each test.

Size, Salinity, and Temperature Effects

The influence of salinity and temperature was tested on the oxygen consumption and osmoregulation of two sizes of *P. aztecus*. Three test salinities (10, 20, 30‰) and four temperatures (18°, 23°, 28°, 33° C) were selected to represent ranges that shrimp may experience in estuaries.

Shrimp were caught and maintained in salinities approximating 20‰; after acclimation to room temperature (23°-25° C) in the laboratory, shrimp of each size class were distributed equally among tanks of 10, 20, and 30‰ S. Transferred shrimp experienced no difficulties adjusting to a 10‰ S change at 23°-25° C. Ambient laboratory temperature was lowered to 18° C and maintained for a week. After oxygen consumption or hemolymph data were obtained from acclimated shrimp, ambient temperature was gradually raised for the next test and the procedure repeated. Four to five days appeared to be necessary to raise the temperature from 28° to 33° C; shrimp mortality increased with faster acclimation rates.

Shrimp were tested in pairs because two shrimp of the smaller size were necessary to cause approximately a 1 ppm oxygen concentration difference between the probes at the tested flow rates. A 1 ppm difference minimized percentage error caused by translating data from the strip-chart recorder and permitted enough flow through the test chamber to avoid oxygen depletion and excreta buildup. An inverted plastic bucket was placed over the chamber during tests to preclude visual disturbances and to reduce light (<10 lm m^{-2}).

Each of the 24 treatment combinations (2 sizes $\times$ 3 salinities $\times$ 4 temperatures) was replicated seven or eight times, and each test lasted 2 h. Acclimated shrimp were selected completely at random without replacement for each test. Therefore the oxygen consumption of a minimum of seven pairs of different shrimp was obtained for each treatment combination. To allow shrimp time to acclimate to the test chamber, data obtained during the first hour were disregarded. Data collected during the second hour were divided into four 15-min periods and the average oxygen consumption for each period was calculated. An ANOVA employing a split plot in a completely randomized design with a $2 \times 3 \times 4$ factorial arrangement as the whole plots and period as the subfactor was computed on the data. The effects of the treatments (size, salinity, temperature), the periods, and the interactions on the oxygen consumption rates were evaluated. If a significant difference was found, then orthogonal comparisons (Snedecor and Cochran 1967) were made to explain more specifically the differences among the treatments, periods, and their interactions. Data plotted in the graphs are the average oxygen consumption during the last ½ h (the third and fourth periods) only.

Shrimp for the osmoregulation studies were caught between 20 March and 20 April 1974 at Airplane Lake. After shrimp were acclimated in the laboratory, hemolymph samples were obtained by puncturing the dorsal arthroidal membrane (just anterior to the first abdominal segment) and bleeding no less than 0.2 ml directly into cuvettes. Cuvettes were sealed with Parafilm to prevent evaporation. The least amount of hemolymph necessary for accurate osmolality determination was 0.2 ml and was obtained from each 6.7 g shrimp; however, two 3.7 g shrimp were needed to collect the minimum volume. Osmolality was measured within 1.5 h with an Osmette. Five samples were tested for each treatment combination except for the following instances: 6.7 g shrimp at 18° C and 10‰ S—three samples; 3.7 g shrimp at 33° C and 10, 20, 30‰ S—four samples; and 6.7 g shrimp at 18° and 28° C and 30‰ S—four samples. Hemolymph was not centrifuged, and little difficulty was experienced in obtaining repeatable readings with the Osmette.

Data were analyzed by an ANOVA employing a $2 \times 3 \times 4$ factorial arrangement in a completely randomized design, and orthogonal comparisons were made on treatment combinations with significant differences. Correlations between hemolymph concentration and oxygen consumption data at corresponding size, salinity, and temperature combinations were made.

RESULTS

Diurnal Effects

Mean oxygen consumption rates ranged from 0.18 to 0.30 mg $O_2 \cdot g\ wet\ m^{-1} \cdot h^{-1}$ among the eight

3-h periods (Table 1), but were not found to be significantly different. The mean oxygen consumption rates for individual shrimp during the 24-h test varied from 0.20 to 0.38 mg $O_2 \cdot g$ wet $m^{-1} \cdot h^{-1}$ and were significantly different (Table 1).

TABLE 1.—Mean diurnal oxygen consumption rates (mg $O_2 \cdot g$ wet $m^{-1} \cdot h^{-1}$) of five *Penaeus aztecus*; m = mass.

Time	Size (g) of individual test shrimp					Mean O_2 consumption per period[1]
	6.1	7.3	6.3	5.9	6.7	
0630-0930	0.18	0.38	0.49	0.17	0.25	0.29
0930-1230	.48	.14	.39	.18	.13	.26
1230-1530	.32	.16	.41	.22	.14	.25
1530-1830	.18	.18	.26	.12	.16	.18
1830-2130	.37	.21	.30	.32	.25	.29
2130-0030	.34	.18	.34	.23	.29	.28
0030-0330	.32	.15	.40	.28	.28	.29
0330-0630	.33	.20	.41	.28	.28	.30
Mean O_2 consumption per 24 h[2]	.32	.20	.38	.23	.22	.27

[1] Differences among time periods not significant
[2] Differences among shrimp highly significant ($P < 0.01$)

Light; Reduced Light Effects

Mean oxygen consumption rates and standard error for seven shrimp tested in light compared with reduced light were 0.25±0.09 and 0.17±0.09 mg $O_2 \cdot g$ wet $m^{-1} \cdot h^{-1}$ and were not found to differ significantly.

Disturbance Effects

The mean oxygen consumption rate of 6.7 g shrimp after disturbance was 0.56±0.05 mg $O_2 \cdot g$ wet $m^{-1} \cdot h^{-1}$ and 4.3 times higher than that (0.13±0.01 mg $O_2 \cdot g$ wet $m^{-1} \cdot h^{-1}$) for resting shrimp. This difference was highly significant.

Crowding Effects

Mean oxygen consumption rates and standard error for 3.7 g *P. aztecus* tested singly and in pairs were 0.50±0.06 and 0.41±0.05 mg $O_2 \cdot g$ wet $m^{-1} \cdot h^{-1}$. These differences were not found to be significant. One or two 3.7 g shrimp in the test chamber resulted in an average of 0.035 or 0.071 g of shrimp cm^{-2} of chamber floor and 0.015 or 0.031 g of shrimp cm^{-3} of chamber volume.

Mean oxygen consumption rates and standard error of 6.7 g *P. aztecus* tested singly and in groups of two, three, and four were 0.30±0.04, 0.37±0.02, 0.35±0.03, and 0.29±0.02 mg $O_2 \cdot g$ wet $m^{-1} \cdot h^{-1}$, respectively. These differences were not statistically significant. One, two, three, or four 6.7 g shrimp in the test chamber represented 0.064, 0.126, 0.188, or 0.247 g of shrimp cm^{-2} and 0.028, 0.054, 0.081, or 0.107 g of shrimp cm^{-3}, respectively.

Size, Salinity, and Temperature Effects

In the factorial test, size and temperature were the only significant main effects, but salinity-size and salinity-temperature effects were significant interactions. (Figure 1, Table 2). The smaller

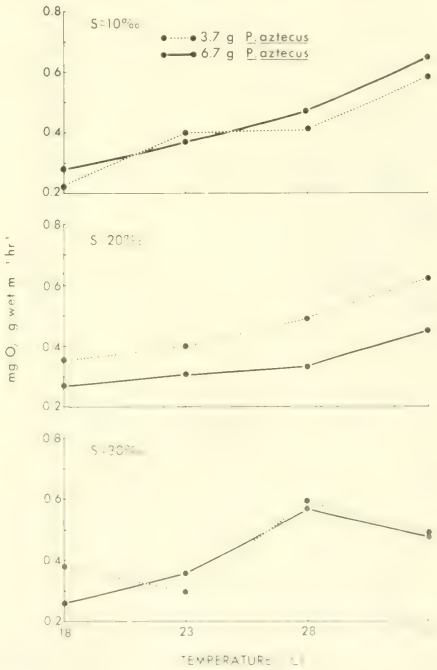


FIGURE 1.—Mean oxygen consumption rate of 3.7 and 6.7 g *Penaeus aztecus* vs. temperature at salinities of 10, 20, and 30‰.

shrimp consumed more oxygen per unit mass (0.44 mg $O_2 \cdot g$ wet $m^{-1} \cdot h^{-1}$) than did the larger shrimp (0.40 mg $O_2 \cdot g$ wet $m^{-1} \cdot h^{-1}$), but this difference was confined to salinities of 20‰ as shown by the salinity-size interaction (Figure 1, Tables 2, 3). In 20‰ S, the 3.7 g shrimp consumed an average of 0.46 mg $O_2 \cdot g$ wet $m^{-1} \cdot h^{-1}$, and the 6.7 g shrimp consumed about 0.34 mg $O_2 \cdot g$ wet $m^{-1} \cdot h^{-1}$.

TABLE 2.—Analysis of variance of the effects of size, salinity, temperature, and period on the mean oxygen consumption rates of *Penaeus aztecus*.

Source of variation	df	Mean square[1]
Size	1	0.3089*
Salinity	2	.0333
Salinity-size	2	.3922**
10‰:3.7 vs. 6.7 g shrimp	1	.0554
20‰:3.7 vs. 6.7 g shrimp	1	.9458**
30‰:3.7 vs. 6.7 g shrimp	1	.0480
Temperature	3	2.5200**
18°, 23° vs. 28°, 33° C	1	6.6970**
18° vs. 23° C	1	.3254*
28° vs. 33° C	1	.4532*
Temperature-size	3	.0172
Salinity-temperature[2]	6	.2744**
10‰:T_l	1	4.2317**
T_q	1	.0100
T_c	1	.0583
20‰:T_l	1	1.6643**
T_q	1	.1327
T_c	1	.0133
30‰:T_l	1	1.7817**
T_q	1	.1393
T_c	1	1.0509**
Size-salinity-temperature	6	.0636
Error (a)	161	.0597
Period:	3	.0838**
Periods 1, 2 vs. periods 3, 4	1	.2024**
Period 1 vs. period 2	1	.0266**
Period 3 vs. period 4	1	.0132**
Size period	3	.0023
Salinity period	6	.0005
Size-salinity period	6	.0001
Temperature period	9	.0048
Size-temperature period	9	.0019
Salinity-temperature period	18	.0031
Size-salinity-temperature period	18	.0007
Error (b)	481	.0017

[1]* = $P<0.05$; ** = $P<0.01$.
[2]Subscripts: l = linear; q = quadratic; c = cubic.

TABLE 3.—Mean oxygen consumption rates of *Penaeus aztecus* for the salinity-size interactions; m = mass.

S (‰)	Size (g)	n	mg O_2 / g wet $m \cdot h$	SE
10	3.7	127	0.411	0.022
10	6.7	120	.442	.022
20	3.7	127	.465	.022
20	6.7	116	.338	.023
30	3.7	124	.436	.022
30	6.7	124	.408	.022

The average oxygen consumption rate increased significantly with increasing temperature, from 0.29 mg $O_2 \cdot$g wet $m^{-1} \cdot h^{-1}$ at 18° C to 0.55 mg $O_2 \cdot$g wet $m^{-1} \cdot h^{-1}$ at 33° C (Table 4). At each salinity oxygen consumption increased linearly with temperature, except at 30‰, where oxygen consumption peaked at 28° C and decreased significantly at 33° C (Figure 1, Table 2).

Oxygen consumption rates differed significantly among periods (Table 2). Rates during the first 15-min period averaged 0.44 mg $O_2 \cdot$g wet $m^{-1} \cdot h^{-1}$ and decreased to an average of 0.40 mg $O_2 \cdot$g wet $m^{-1} \cdot h^{-1}$ during the fourth 15-min period (Table 5). Significant differences of oxygen consumption rates among period interactions were not found (Table 2).

TABLE 4.—Mean oxygen consumption rates of *Penaeus aztecus* for each test temperature; m = mass.

T (°C)	n	mg O_2 / g wet $m \cdot h$	SE
18	187	0.293	0.018
23	184	.352	018
28	183	.479	.018
33	184	.549	018

TABLE 5.—Mean oxygen consumption rate of *Penaeus aztecus* during four consecutive 15-min periods after 1 h acclimation in respirometer chamber; m = mass.

15-min period	n	mg O_2 / g wet $m \cdot h$	SE
First	184	0.443	0.003
Second	184	.426	.003
Third	186	.407	.003
Fourth	184	.395	.003

When hemolymph osmolality was analyzed for shrimp acclimated to the same conditions as previously described, size and salinity were significant main effects; and salinity-size, temperature-size, and salinity-temperature effects were significant interactions (Figure 2, Table 6). The mean hemolymph osmolality of 3.7 g shrimp was significantly higher than that of 6.7 g shrimp (Tables 6, 7), but this difference was found only in combinations that included 30‰ S or 33° C. In 30‰ S the smaller shrimp's hemolymph osmolality averaged over all temperatures was 796 mOsm (milliosmoles) compared with 753 for the larger shrimp. At 33° C the same comparison averaged over all salinities was 734 and 678 mOsm (Figure 2).

The mean hemolymph osmolality increased with increasing salinity (616, 696, and 774 mOsm at 10, 20, and 30‰, respectively; Table 7). At each salinity, the effect of increasing temperature on the shrimp's hemolymph osmolality was tested. Significant linear responses were obtained at 10 and 30‰ (Table 6, Figure 3). Significant correlations were not found between hemolymph osmolality and oxygen consumption rates.

DISCUSSION

Sources of Variability

Many complicating variables must be considered in attempting to obtain the standard metabolism of penaeid shrimp. Physiological rhythms, stage of the molt cycle, and lunar phases

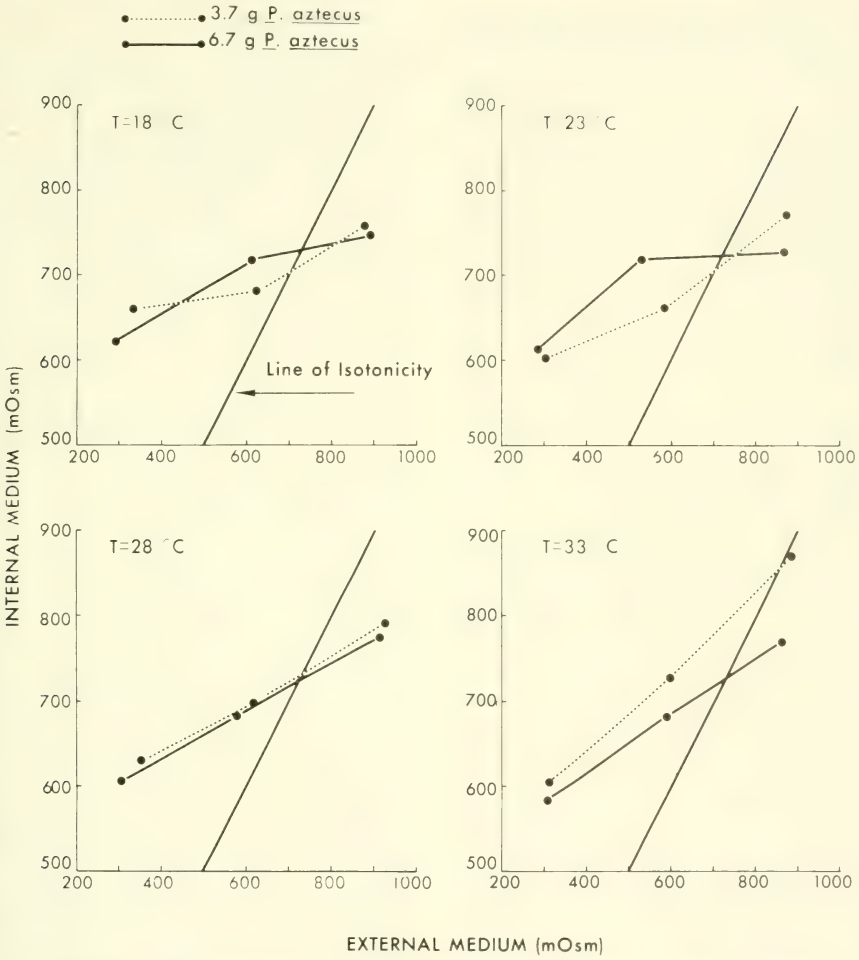


FIGURE 2.—Mean hemolymph osmolality (mOsm) of 3.7 and 6.7 g *Penaeus aztecus* vs. temperatures at 18°, 23°, 28°, and 33° C.

may complicate the ideal of testing uniform subjects under similar conditions. In addition, the effects of spontaneous activity often mask any differences of metabolism resulting from the effects of osmoregulation, size, temperature, etc. In the present study, attempts to eliminate molt-stage differences were made by testing a minimum of seven pairs of shrimp. Because integumental changes occur at least 70% of the time between successive molts for decapods (Passano 1960), the testing of only intermolt, acclimated animals would have been nearly impossible. Most of the shrimp tested, however, should have been in a stage other than immediate premolt, and newly molted shrimp were not tested. Therefore it is assumed that most of the test animals were at a molt stage that affected the total oxygen consumption relatively little.

TABLE 6.—Analysis of variance of the effects of size, salinity, and temperature on the osmolality of *Penaeus aztecus* hemolymph.

Source of variation	df	Mean square[1]
Size	1	9,343*
Salinity	2	231,198**
10, 20 vs. 30‰	1	332,414**
10 vs. 20‰	1	121,516**
Salinity-size	2	5,836*
10‰:3.7 vs. 6.7 g shrimp	1	4,076
20‰:3.7 vs. 6.7 g shrimp	1	624
30‰:3.7 vs. 6.7 g shrimp	1	16,781**
Temperature	3	2,734
Temperature-size	3	4,899*
18° C: 3.7 vs. 6.7 g shrimp	1	447
23° C: 3.7 vs. 6.7 g shrimp	1	367
28° C: 3.7 vs. 6.7 g shrimp	1	4,136
33° C: 3.7 vs. 6.7 g shrimp	1	20,449**
Salinity-temperature[2]	6	5,597**
10‰:T_l	1	8,959*
T_q	1	231
T_c	1	3,110
20‰:T_l	1	12
T_q	1	1,523
T_c	1	12
30‰:T_l	1	23,623**
T_q	1	2,368
T_c	1	1,065
Size-salinity-temperature	6	2,061
Error (a)	89	1,231

[1] * = $P<0.05$; ** = $P<0.01$

[2] Subscripts: l = linear; q = quadratic; c = cubic.

TABLE 7.—Mean hemolymph osmolality of *Penaeus aztecus* in relation to size and salinity of acclimation water.

Variable	*n*	Hemolymph (mOsm)	SE	Osmolality of external medium (mOsm)
Size, g:				
3.7	56	703	4.7	606
6.7	57	688	4.6	584
Salinity, ‰:				
10	37	616	5.8	310
20	39	696	5.6	590
30	37	774	5.8	886

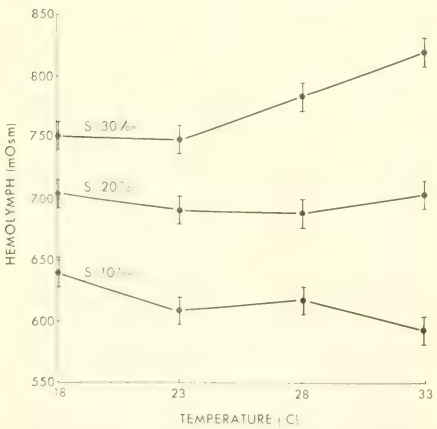


FIGURE 3.—Mean hemolymph osmolality of *Penaeus aztecus* vs. temperature at salinities of 10, 20, and 30‰.

Although no significant time-of-day differences were found (Table 1), efforts were made to test equal numbers of shrimp in the morning and afternoon at each treatment combination. Evidence indicates that shrimp are influenced by lunar cycles (Wheeler 1937; Racek 1959; Aaron and Wisby 1964; Wickham 1967; Hughes 1972; Bishop and Herrnkind 1976), but in the present studies, we assumed that lunar influences on the oxygen consumption were negligible because of acclimation periods. Subrahmanyam (1976) obtained results indicating the presence of an oxygen consumption rhythm in pink shrimp that coincided with the tidal cycle, but this rhythm waned after the shrimp were maintained for a week in captivity.

Because of the absence of standardized techniques for measuring routine oxygen consumption of poikilotherms, many of the previous studies on the oxygen consumption of penaeid shrimp are of limited usefulness. Frequently pertinent circumstances relating to acclimation time and (or) test conditions were not reported (Subrahmanyam 1962; Zein-Eldin and Klima 1965; Weerasinghe and Arudpragasam 1967; Steed and Copeland 1967), and closed chambers were used in most published studies. Consequently, test animals could not acclimate to test chamber conditions and probably exhibited increased activity.

In our studies, the shrimp's activity was minimized by several methods: first, the test animals were acclimated to a specific test salinity-temperature combination for at least a week prior to testing; second, the shrimp were allowed to acclimate to the test chamber for an hour before data were collected; and third, an inverted opaque plastic bucket was placed over the test chamber to reduce the light and to prevent disturbances from human activity in the laboratory.

Reducing the light to the test chamber reduced the mean oxygen consumption (0.25 vs. 0.17 mg $O_2 \cdot g$ wet $m^{-1} \cdot h^{-1}$) although the effect was not statistically significant. The hour acclimation prior to taking data was not enough time to allow the shrimp to adjust to the test chamber because the oxygen consumption rate for each 15-min period continued to decline throughout the second hour (Tables 2, 5). Although the average oxygen consumption rate decreased significantly during each subsequent 15-min period of the second hour of testing, the overall rate change was small, an 11% decrease between the first and last period. The rate change was consistent across all treatments and unrelated to the treatment effects because no

significant differences were found among any of the period interactions (Table 2); thus the effects of size, salinity, and temperature are independent of acclimation time. The average oxygen consumption data for each treatment combination in Table 3 and Figure 1 are slightly higher than would be expected for shrimp completely acclimated to the test chamber, however. Egusa (1961) found that the oxygen consumption rate of *P. japonicus* stabilized after about 3 h. Acclimation time to test conditions may have been reduced if fine-grained substrate had been included in the test chamber. Penaeid shrimp exhibit arrhythmic activity when they cannot bury in substrate (Racek 1959; Moller and Jones 1975).

Because shrimp may be both oxygen conformers and regulators, crowding could profoundly influence their oxygen consumption by increasing the extent of activity. We found no significant oxygen consumption rate differences between one and two 3.7 g *P. aztecus* or among one, two, three, and four 6.7 g *P. aztecus* when compared on a per gram wet mass basis, and believe that testing two shrimp simultaneously did not appreciably affect their oxygen consumption rates. Subrahmanyam (1976) noticed no differences in activity when testing pink shrimp singly or in pairs.

Salinity Effects on Oxygen Consumption and Osmoregulation

The influence of salinity on the life habits of penaeid shrimp has received considerable attention (Panikkar 1951, 1968; Gunter and Hildebrand 1954; Zein-Eldin 1963; Gunter et al. 1964; Parker 1970). Panikkar (1951) suggested that high salinity may be necessary for ovarian development, but its importance still remains unknown. Life cycles of the three penaeid shrimp important commercially in the Gulf are similar (Williams 1965), but juvenile white shrimp, *P. setiferus*, are reported to prefer salinities <10‰; juvenile brown shrimp, salinities between 10 and 20‰; and juvenile pink shrimp, salinities >18‰ (Gunter et al. 1964). Adaptation to low salinities is highly developed in young penaeids, and juveniles are more widely distributed in estuaries than are adults. Thus, osmoregulatory capabilities may influence emigration of subadults from estuaries (Panikkar 1968). Zein-Eldin (1963) obtained good growth and survival for postlarval *P. aztecus* at 2, 5, 10, 25, and 40‰, and concluded that salinity per se may not directly affect growth during the estuarine portion of their life cycle. These postlarvae were grown only to sizes <0.2 g (Zein-Eldin 1963), so the effects of low salinity on growth rate during a substantial portion of their life cycle remains uninvestigated.

Brown shrimp were hyperosmotic regulators in 10 and 20‰ S and hypoosmotic regulators in 30‰ S. Depending on salinity and temperature, hemolymph osmolality was maintained at concentrations approximating 600-900 mOsm (Figure 2). These results agree with those of Williams (1960) and McFarland and Lee (1963). Thus *P. aztecus* cannot be considered a perfect regulator, but it differs substantially from nonregulators. Panikkar (1968) considered homoiosmotic regulation to be one of the most advanced capabilities of marine invertebrates.

Oxygen consumption would be expected to increase for osmoregulators as the osmotic difference between the shrimp's hemolymph and its environment increased because metabolism would increase to maintain a constant hemolymph concentration. Energy expenditure for osmoregulation depends on the species and is related to temperature as well as other variables (see reviews by Kinne 1964, 1966, 1967).

There is conflicting evidence as to whether important energy expenditures are necessary to maintain homoiosmotic hemolymph (Schwabe 1933; Lofts 1956; Rao 1958; Dehnel 1960). In our tests hemolymph osmolalities of *P. aztecus* were significantly affected by salinity, but the energy expenditures for osmoregulation after acclimation were small in relation to total metabolic rate. Other studies on euryhaline decapods show that salinity does not have pronounced effects on oxygen consumption if the experimental animals are acclimated to the test salinities and if test salinities are not too extreme (Lofts 1956; Rao 1958; Kader 1962; Kutty et al. 1971).

Venkataramiah et al. (footnote 4) acclimated brown shrimp to 15‰ S at 25° C and measured oxygen consumption rates after salinity was changed to 2, 5, 10, 15, 25, and 36‰. Metabolic rates increased initially, but generally tended toward that of acclimation conditions after a day unless deviations from acclimation salinity were substantial, i.e., 2, 5, and 36‰. Salinity changes in the respirometer were made over a 1-h period, however, and may have been too rapid and (or) extreme for the shrimp's capacity to adjust. Venkataramiah et al. (footnote 4) found that blood hemolymph required 6 h to achieve osmotic stabil-

ity when shrimp were transferred from 15 to 2 or 36‰ S; osmotic stability was achieved in 2 h after transfer from 15 to 5, 10, 15, or 25‰ S.

Highest catch rates for brown shrimp were determined by Copeland and Bechtel (1974) to occur in salinities from <4 to >35‰. This lower limit is slightly less than the range of salinities (5-8‰) suggested by Khlebovich (1968) at which ion ratios change from typically freshwater to marine. Therefore it appears that if juvenile or subadult shrimp were acclimated to salinities that are typically marine (8-35‰), oxygen consumption rates will not reflect any significant increased energy demands necessary for osmoregulation. Table 8 summarizes oxygen consumption rates of penaeid shrimp that have been acclimated to and tested at various salinity-temperature combinations. Routine and standard rates vary from 0.14 to 0.75 mg $O_2 \cdot g$ wet $m^{-1} \cdot h^{-1}$.

Shrimp Size Effects on Oxygen Consumption and Osmoregulation

The effects of size on an animal's oxygen consumption are apparent for individuals ranging from 1 to 1,000 g (Zeuthen 1947). Generally, a large

TABLE 8.—Oxygen consumption of penaeid shrimps; some data converted to allow uniform reporting. Temperature (T) in degrees Celsius, salinity (S) in parts per thousand, and mass (m) of live shrimp in grams. Genera *Metapenaeus* and *Penaeus* abbreviated as *M.* and *P.*

	Acclimation			Test		Size	Metabolic	mg O_2	
Species	T	S	Days	T	S	(g)	state	g wet $m \cdot h$	Source
M. monoceros[1]	29	35	>3	29	30	0.53	Routine?	1.34	Kader (1962)
	31	33	1½	31	33	2-6	Routine	.75	Rao (1958)
	31	20	1½	31	17	2-6	Routine	.75	Rao (1958)
P. aztecus	—	—	Several	—	—	4-7	Routine?	.39	Zein-Eldin and Klima (1965)
	—	32	½	—	32	—	Routine?	.3	Steed and Copeland (1967)
	18	10	>7	18	10	3.7	Routine	.22	Bishop (1974)
	18	20	>7	18	20	3.7	Routine	.35	Bishop (1974)
	18	30	>7	18	30	3.7	Routine	.38	Bishop (1974)
	23	10	>7	23	10	3.7	Routine	.40	Bishop (1974)
	23	20	>7	23	20	3.7	Routine	.40	Bishop (1974)
	23	30	>7	23	30	3.7	Routine	.30	Bishop (1974)
	28	10	>7	28	10	3.7	Routine	.44	Bishop (1974)
	28	20	>7	28	20	3.7	Routine	.49	Bishop (1974)
	28	30	>7	28	30	3.7	Routine	.59	Bishop (1974)
	33	10	>7	33	10	3.7	Routine	.59	Bishop (1974)
	33	20	>7	33	20	3.7	Routine	.62	Bishop (1974)
	33	30	>7	33	30	3.7	Routine	.49	Bishop (1974)
	18	10	>7	18	10	6.7	Routine	.28	Bishop (1974)
	18	20	>7	18	20	6.7	Routine	.27	Bishop (1974)
	18	30	>7	18	30	6.7	Routine	.26	Bishop (1974)
	23	10	>7	23	10	6.7	Routine	.37	Bishop (1974)
	23	20	>7	23	20	6.7	Routine	.31	Bishop (1974)
	23	30	>7	23	30	6.7	Routine	.35	Bishop (1974)
	28	10	>7	28	10	6.7	Routine	.47	Bishop (1974)
	28	20	>7	28	20	6.7	Routine	.33	Bishop (1974)
	28	30	>7	28	30	6.7	Routine	.57	Bishop (1974)
	33	10	>7	33	10	6.7	Routine	.64	Bishop (1974)
	33	20	>7	33	20	6.7	Routine	.45	Bishop (1974)
	33	30	>7	33	30	6.7	Routine	.48	Bishop (1974)
	18	15	7	18	15	~6	Standard	.12	Venkataramiah et al. (text footnote 4)
	25	15	7	25	15	~6	Standard	.18	Venkataramiah et al. (text footnote 4)
	32	15	7	32	15	~6	Standard	.38	Venkataramiah et al. (text footnote 4)
P. duorarum	—	32	½	—	32	—	Routine	.14	Steed & Copeland (1967)
	25	20	1	25	20	0.44	Standard	.59	Subrahmanyam (1976)
	25	20	1	25	20	0.44	Active	1.19	Subrahmanyam (1976)
	25	20	1	25	20	0.52	Standard	.76	Subrahmanyam (1976)
	25	20	1	25	20	0.52	Active	1.54	Subrahmanyam (1976)
	25	20	1	25	20	1.68	Standard	.26	Subrahmanyam (1976)
	25	20	1	25	20	1.68	Active	.47	Subrahmanyam (1976)
	25	20	1	25	20	3.65	Standard	.47	Subrahmanyam (1976)
	25	20	1	25	20	3.65	Active	.57	Subrahmanyam (1976)
	25	20	1	25	20	9.66	Standard	.18	Subrahmanyam (1976)
	25	20	1	25	20	9.66	Active	.26	Subrahmanyam (1976)
	25	20	1	25	20	11.0	Standard	.26	Subrahmanyam (1976)
	25	20	1	25	20	11.0	Active	.30	Subrahmanyam (1976)
P. indicus	28	15	—	28	15	2.4-3.7	Routine	.57	Subrahmanyam (1962)
	28	15	—	28	15	5.1-7.8	Routine	.36	Subrahmanyam (1962)
	30	36	14	30	36	2.7	Routine	.7	Kutty (1969)
	28	21	5	28	21	0.1	Routine	.9	Kutty et al. (1971)
P. japonicus	23	28	7-14	23	28	2.4-3.7	Standard	.18	Egusa (1961)
	23	28	7-14	23	28	4.6-6.2	Standard	.15	Egusa (1961)
P. semisulcatus	30	36	14	30	36	17.3	Routine	.35	Kutty (1969)
P. setiferus	25	22	14	25	25	0.04	Routine?	1.60	Green et al. (1976)

[1]Tested at 63% oxygen saturation.

individual consumes more oxygen than a smaller one, but its rate of oxygen consumption per unit mass is less (Mill 1972). In our study this generalization was found for shrimp only at 20‰ S. Although it is not known why this difference was evident at only one salinity, it should be noted that among the six salinity-size treatment combinations, the lowest as well as the highest metabolic rates occurred at 20‰ S (Figure 4). It is possible that the 3.7 g shrimp were more active than "routine" in the test chamber and that the 6.7 g shrimp were less active than "routine." Tests for both sizes at each temperature were conducted within a few days of each other, and we believe that the time element was not responsible for the observed difference. Each salinity-size combination is the average of approximately 30 tests, and the possibility of obtaining the results by chance is small. The data in Table 8 indicate decreasing metabolic rate (per unit mass) with increasing size, although extreme variability exists.

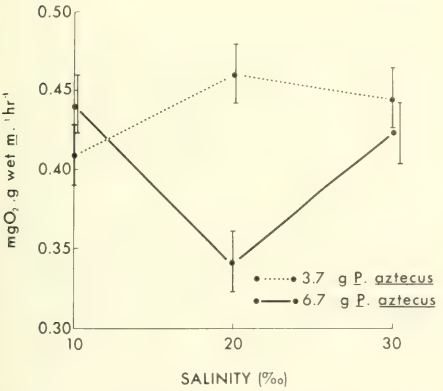


FIGURE 4.—Mean oxygen consumption rate (average for all test temperatures) of 3.7 and 6.7 g *Penaeus aztecus* at salinities of 10, 20, and 30‰.

As shrimp increase in size in the estuary, they move to higher, more stable salinities (Weymouth et al. 1933; Gunter 1945, 1950; Williams 1960; Bishop and Shealy[7]). This movement may be, in part, a response to a decrease in osmoregulatory ability with increasing size. Only two sizes of shrimp were tested, and both sizes were obtained from the same locality (often from the same trawl tow). Thus osmoregulation differences would not be anticipated to be large. The larger shrimp appear to be better regulators in hyperosmotic salinity and at high temperatures. The slopes of the hemolymph data over test salinities at 33° C for the 3.7 and 6.7 g shrimp were 0.47 and 0.33, indicating that the larger shrimp maintained homoiosmoticity to a better degree than did the smaller shrimp at a temperature approaching an environmental extreme (Figure 2).

Some of our test conditions and those of Williams (1960) are nearly identical, and hemolymph data from shrimp acclimated to similar conditions are comparable. Hemolymph data from both 3.7 and 6.7 g shrimp were averaged to be compatible with Williams' (1960) juvenile *P. aztecus* (42-100 mm TL). At 28° C and 10, 20, and 30‰ S, we obtained average hemolymph osmolalities of 619, 689, and 785 mOsm, respectively, whereas Williams obtained values approximating 657, 804, and 825 mOsm. Williams' values are somewhat higher than ours, but physiological differences in populations, analytical techniques, or acclimation history of test animals could be responsible.

Because small shrimp (3.7 g) may encounter highly variable salinities, they may be capable of tolerating relatively variable hemolymph osmolalities and their osmoregulatory processes may not be as capable of homoiosmoregulation as those of larger shrimp. This implies that varying salinities would be more expensive energetically for larger shrimp and partially responsible for their offshore movement prior to maturity.

Temperature Effects on Oxygen Consumption and Osmoregulation

Metabolic rate of most poikilotherms is related to temperature (Prosser 1973). The lowest test temperature that we used (18° C) approached as closely as our facilities permitted the 16° C at which *P. aztecus* is reported to exhibit little growth (St. Amant et al. 1966). The highest test temperature approaches the shrimp's lethal limit (Zein-Eldin and Griffith 1969) and is seldom experienced in Louisiana estuaries. The oxygen consumption rates of shrimp increased linearly as temperature increased, and rates for both sizes increased in a similar manner (Figure 1).

[7] Bishop, J. M., and M. H. Shealy, Jr. 1977. Biological observations on commercial penaeid shrimps caught by bottom trawl in South Carolina estuaries, February 1973 - January 1975. S.C. Wildl. Mar. Resour. Dep., Mar. Res. Div., Tech. Rep. 25, 97 p.

The Q_{10}'s [oxygen consumption at (T + 10) ° C/oxygen consumption at T° C] are presented in Table 9. Although there are minor differences at different temperature ranges, the average Q_{10}'s are nearly equal and very close to the average 1.7 obtained by Scholander et al. (1953) for *P. brasiliensis* tested at 25° and 30° C. Wolvekamp and Waterman (1960) stated that generally Q_{10} values increase as the temperature decreases, but an increase was not obvious in this study.

TABLE 9.—Q_{10}'s for two sizes of *Penaeus aztecus*; oxygen consumption data averaged over all test salinities.

Size (g)	Temperature (° C)	Q_{10}
3.7	18-28	1.59
3.7	23-33	1.63
6.7	18-28	1.71
6.7	23-33	1.63
Mean	18-28	1.65
Mean	23-33	1.63

Temperature effects at tested salinities were not uniform. In 10 and 20‰ S, oxygen consumption increased significantly as temperature increased (Figure 1, Table 2), but in 30‰ S, oxygen consumption peaked at 28° C and decreased at 33° C. This reduction indicates a possible detrimental effect on *P. aztecus* when both salinity and temperature are high. The osmoregulatory abilities of *P. aztecus* are reduced at 33° C (Figures 2, 3), and salinity effects appear to become increasingly important. Other studies have also indicated reduced responses of *P. aztecus* tested at high temperatures. Survival of juveniles (10-50 mm TL) was <80% at temperatures >28° C at 25‰ S (Zein-Eldin and Aldrich 1965; Zein-Eldin and Griffith 1969). Rates of growth (mass) of postlarvae in salinities >25‰ were less at 32° C than at 25° C (Zein-Eldin and Aldrich 1965). Brown shrimp acclimated to 32° C were more sensitive to temperature change than those acclimated to 18° or 25° C and showed reduced osmoregulatory abilities in salinities <10‰ (Venkataramiah et al. footnote 4).

The possibility exists that oxygen consumption rates at 33° C and 30‰ S are a reflection of reduced dissolved O_2 concentration. That is, at 33° C, oxygen is less soluble in 30‰ S than in 10 or 20‰ S, and the shrimp's oxygen consumption may be proportional to the oxygen concentration. To test this hypothesis, the difference between the average oxygen consumption in 20 and 30‰ S at 33° C was calculated and compared with the difference between the oxygen available in the test chamber at 20 and 30‰ at 33° C (Table 10). The decrease of

TABLE 10.—Calculation of oxygen available to *Penaeus aztecus* and consumed at 20 and 30‰ salinity (S) and 33° C; m = mass.

O_2 available (mg h^{-1}) at 20‰ S	15.62
O_2 available (mg h^{-1}) at 30‰ S	14.06
Difference (mg O_2 h^{-1})	1.56
Average O_2 consumption mg · g wet m^{-1} h^{-1} for shrimp at 20‰ S	0.54
Average mass (g) of shrimp	5.10
Average O_2 consumption (mg h^{-1}) per shrimp	2.75
Average O_2 consumption mg · g wet $m^{-1} \cdot h^{-1}$ for shrimp at 30‰ S	0.49
Average mass (g) of shrimp	5.47
Average O_2 consumption (mg h^{-1}) per shrimp	2.68
O_2 consumption difference between 20 and 30‰ S (mg O_2 h^{-1})	0.07

total oxygen consumption between 20 and 30‰ was <0.1 mg h^{-1} and is not of similar magnitude to the oxygen-available difference of 1.56 mg h^{-1}; the differences indicate that *P. aztecus* is an oxygen regulator. Also the saturated oxygen concentration at 30‰ S and 33° C is well above the stress level of 2 ppm obtained by Egusa (1961) for *P. japonicus*. Therefore the decrease in dissolved oxygen resulting from the increased salinity does not appear to be responsible for the reduced rate of oxygen consumption of brown shrimp in 30‰ S and 33° C.

As temperature increased to 33° C, hemolymph osmolality tended toward that of the external medium for shrimp tested in 10 and 30‰ S (Figure 3). Williams (1960) found the osmoregulatory abilities of *P. aztecus* were significantly less at 8.8° C than at 28° C. Thus it appears that as temperature approaches environmental extremes, osmoregulatory abilities are impaired, and shrimp tend toward osmoconformity. *Penaeus aztecus* was able to maintain homoiosmoticity at 20‰ over the tested temperatures (Figure 3), indicating that at high temperatures (33° C) and a moderate salinity, osmoregulatory processes are not adversely affected.

Energy Considerations

The metabolic energy expenditure of shrimp can be calculated from knowledge of their oxygen consumption rates and their metabolic substrate (indirect calorimetry). Because shrimp are omnivorous (Williams 1955; Mistakidis 1957; Eldred et al. 1961; Pérez Farfante 1969; Moriarty 1977), a combination of carbohydrate, lipid, and protein as the shrimp's metabolic substrate should give a reasonable estimate of the oxygen-consumption/energy-expenditure relationship. At standard conditions, combustion of 1 g of carbohydrate, lipid, or protein with 1 l of oxygen yields 5,007,

4,686, or 4,500 cal, respectively (Giese 1968). The caloric value of each of these sources varies <6% from the mean. Therefore, for every milligram of oxygen consumed, about 3.31 cal will be liberated. A 6.7 g *P. aztecus* utilizes 0.87 and 3.75 mg O_2 h^{-1} at rest and during activity at 25° C, which translates to 2.88 and 12.41 cal h^{-1}. (The caloric expenditure during activity is calculated from the maximum oxygen consumption over a 15-min period.) Other average energy expenditures of *P. aztecus* at selected conditions are presented in Table 11.

TABLE 11.—Mean rates of oxygen consumption and energy expenditures of *Penaeus aztecus* at each test temperature averaged over all test salinities; m = mass.

Size (g)	Temperature (°C)	mg O_2 / g wet m · h	calories / g wet m · h
3.7	18	0.32	1.06
3.7	23	0.36	1.19
3.7	28	0.51	1.69
3.7	33	0.57	1.89
6.7	18	0.27	0.89
6.7	23	0.34	1.13
6.7	28	0.45	1.49
6.7	33	0.53	1.75

About 80% of a penaeid shrimp's mass is water,[8] so the dry mass of a 3.7 and a 6.7 g shrimp approaches 0.74 and 1.34 g, respectively. A gram of dried whole *Metapenaeus monoceros* yields 3,066 cal upon combustion (Qasim and Easterson 1974); thus the energy content of a 3.7 g *P. aztecus* is about 2,269 cal and that of a 6.7 g shrimp, about 4,108.

If a 6.7 g shrimp maintains a resting state for 24 h at 25° C, then a minimum of 69 cal will be utilized just for maintenance. This is about 1.7% of its total caloric content or 0.11 g wet mass equivalent. Therefore, a 6.7 g shrimp must daily assimilate a minimum of 1.7% of its body wet mass of equal caloric value food to maintain itself at rest. If a maximum state of activity were continued for 24 h (oxygen consumption = 0.56 mg $O_2 \cdot g$ wet $m^{-1} \cdot h^{-1}$, then approximately 298 cal would be expended. This is more than 7.2% of the 6.7 g shrimp's total caloric content. Shrimp obviously do not maintain a continuous state of maximum activity, and their mean daily energy expenditure is probably 3-4% of body caloric content.

Oxygen consumption averaged over all test salinities and at 23° and 28° C during the fourth 15-min test period was 0.40 and 0.37 mg $O_2 \cdot g$ wet $m^{-1} \cdot h^{-1}$ for 3.7 and 6.7 g shrimp (Bishop 1974). These two shrimp sizes and water temperatures are characteristic of Barataria Bay, La. during May (St. Amant et al. 1966), and an average oxygen consumption rate of 0.38 mg $O_2 \cdot g$ wet $m^{-1} \cdot h^{-1}$ should be a conservative estimate of routine oxygen consumption for inshore shrimp during this time period. Because *P. aztecus* buries itself in the substrate during the day (Williams 1965), we calculated daily caloric expenditures based on a routine state of metabolism for 12 h and a resting state for 12 h. Using the average value of 0.38 mg $O_2 \cdot g$ wet $m^{-1} \cdot h^{-1}$ for routine oxygen consumption and 0.13 mg $O_2 \cdot g$ wet $m^{-1} \cdot h^{-1}$ for standard metabolism for 5.2 g *P. aztecus* (average of 3.7 and 6.7 g shrimp), a daily caloric expenditure of 105 cal is obtained. This is about 3.3% of a 5.2 g shrimp's caloric content and supports the assumption of a 3-4% expenditure of their body wet mass per 24 h.

St. Amant et al. (1966) estimated that *P. aztecus* grew an average of 1 mm d^{-1} while in the estuaries, which represents a daily gain in wet mass of 0.18 g (Fontaine and Neal 1971) or 110 cal in potential energy.

Because shrimp feed on a variety of materials in the estuary (Williams 1955; Dall 1968; George 1974), assimilation rates probably vary widely depending on the food ingested and its chemical composition. Assimilation efficiency calculated on a mass basis may differ from that based on calories, and a range of efficiencies would be expected in natural conditions. As assimilation efficiency decreases, maintenance energy increases, but the point of diminishing returns is not known. Condrey et al. (1972) determined from laboratory experiments that shrimp of the genus *Penaeus* assimilated 33-74% of the ingested food mass, and Jones (1973) reported 25-40% assimilation rates from shrimp feeding naturally in Airplane Lake. Using extremes of these percentages and assuming that assimilation rates for mass and calories are similar and that *P. aztecus* is primarily a detrital consumer in Louisiana estuaries, first order approximations are possible for daily ingestion rates (Table 12).

Assimilation (A) of food energy must equal the sum of that for respiration (R), stored energy (growth G), and excretion (E) (see Table 12). Assimilated food is derived from food ingested (I). If the energy assimilation efficiency ($A/I \times 100$) is assumed to be 34%, a 5.2 g shrimp must consume about 638 cal d^{-1} at observed growth rates [G +

[8]H. C. Loesch, marine biologist, 1232 Dahlia St., Baton Rouge, LA 70808, unpubl. data 13 November 1974.

$R + E = A$; 110 + 105 + 2 = 217 cal d^{-1}; $I = A/0.34$ = 638 cal d^{-1}]. This is equivalent to 1.10 g wet *Spartina alterniflora* detritus [assuming 3,760 cal/dry g (Gosselink and Kirby 1974) and 84.4% water[9]], or about 20.0% of the shrimp's body mass per day. Daily growth rates of brown shrimp have been reported as rapid as 3.3 mm (Ringo 1965). This is more than three times the rate used for our calculations and would substantially increase the amount of ingested food and consequently the percent of food mass intake relative to body mass.

TABLE 12.—Daily calorie values for energy ingested (I) and that utilized for growth (G), respiration (R), and excretion (E) based on assimilation rates of 25 and 74% for a 5.2 g (live mass) *Penaeus aztecus*.

Assimilation efficiency (%)	G	R	[1]E	I
25	110	105	2	868
74	110	105	2	293

[1]Calculated from Nelson et al. (1977) and Brafield and Solomon (1972).

Qasim and Easterson (1974) obtained caloric assimilation efficiencies as high as 96.84% for *M. monoceros*, but they fed shrimp small particle detritus, which they settled from estuarine waters. This detritus was composed of a substrate of "fine silt and sand" (Qasim and Sankaranarayanan 1972), and its caloric value was nearly an order of magnitude less than that of *S. alterniflora* detritus (Gosselink and Kirby 1974). The low caloric detritus used in Qasim and Easterson's experiments may be responsible for the high assimilation efficiencies (assimilation calculated on ingested mass would probably be less efficient). We believe that the wide range of assimilation efficiencies used in our calculations are representative of most wild shrimp even if efficiencies for ingested mass and calories differ considerably. Also, diets of shrimp are not readily ascertained and more refined estimates may not be practical. Shrimp grown in intensive culture situations and fed a prepared diet, however, exist in relatively stable conditions; energy budgets for these shrimp could be more accurately determined and used to reduce feeding costs and possibly to increase production.

The wide tolerance of *P. aztecus* to temperature and salinity allows it to make maximum use of estuaries. Although we obtained evidence indiciating that larger shrimp can regulate hypoosmotically to a better degree than smaller shrimp, smaller shrimp can readily grow and survive Gulf salinities (Hoese 1960; Zein-Eldin 1963). Thus during years when shrimp populations are unusually dense in estuaries, shrimp can emigrate from the estuaries to Gulf waters at a size less than that of shrimp during average population years. This may reduce competition for space and food in the nursery areas (Parker 1970) and result in greater estuarine shrimp production. The suitability of estuaries as nursery grounds for shrimp results from several important circumstances including food abundance (Zein-Eldin 1963; Copeland and Bechtel 1974), protection (Hoese 1960), cover (Williams 1955; Giles and Zamora 1973), substrate (Williams 1958), absence of competition between juveniles and adults, and to a lesser degree, the shrimp's osmoregulatory abilities.

[9]Unpublished data of senior author.

ACKNOWLEDGMENTS

We thank P. E. Schilling for his consultation on experimental design and analyses of data; J. D. Woodring for use of his osmometer; N. J. Gazaway and L. H. Hodges for typing; C. J. Poche for drafting; D. E. Wohlschlag and anonymous reviewers for editorial comments; and W. B. Stickle, R. D. Adams, and E. M. Bishop for assisting in various ways. N. L. Mickelberry supported and encouraged the senior author throughout this study; her efforts are particularly appreciated. This research was submitted by the senior author in partial fulfillment of the requirements for the degree of Doctor of Philosophy at Louisiana State University. This report is the result of research supported by the Louisiana Sea Grant Program, a part of the National Sea Grant Program maintained by the National Oceanic and Atmospheric Administration, U.S. Department of Commerce.

LITERATURE CITED

AARON, R. L., AND W. J. WISBY.
1964. Effects of light and moon phase on the behavior of pink shrimp. Gulf Caribb. Fish. Inst., Proc. 16th Annu. Sess., p.121-130.

BISHOP, J. M.
1974. The influence of selected conditions on the oxygen consumption and hemolymph osmolality of the brown shrimp, *Penaeus aztecus* Ives. Ph.D. Thesis, Louisiana State Univ., Baton Rouge, 150 p.
1976. A continuous recording, differential respirometer for a closed, flowing seawater system. Oikos 27:127-130.

BISHOP, J. M., AND W. F. HERRNKIND.
1976. Burying and molting of pink shrimp, *Penaeus duorarum* (Crustacea: Penaeidae), under selected photoperiods of white light and UV-light. Biol. Bull. (Woods Hole) 150:163-182.

BRAFIELD, A. E., AND D. J. SOLOMON.
1972. Oxy-calorific coefficients for animals respiring nitrogenous substrates. Comp. Biochem. Physiol. 43A:837-841.

BRETT, J. R.
1970. Fish - the energy cost of living. *In* W. J. McNeil (editor), Marine aquaculture, p. 37-52. Oreg. State Univ. Press, Corvallis.

BRODY, S.
1945. Bioenergetics and growth. Reinhold Publ. Corp., 1023 p.

COCHRAN, W. G., AND G. M. COX.
1957. Experimental designs. 2d ed. Wiley, N.Y., 611 p.

CONDREY, R. E., J. G. GOSSELINK, AND H. J. BENNETT.
1972. Comparison of the assimilation of different diets by *Penaeus setiferus* and *P. aztecus*. Fish. Bull., U.S. 70:1281-1292.

COPELAND, B. J., AND T. J. BECHTEL.
1974. Some environmental limits of six Gulf coast estuarine organisms. Contrib. Mar. Sci. 18:169-204.

CRAMPTON, E. W., AND L. E. HARRIS.
1969. Applied animal nutrition. 2d ed. W. H. Freeman, San Franc., 753 p.

DALL, W.
1968. Food and feeding of some Australian penaeid shrimp. FAO Fish. Rep. 57:251-258.

DEHNEL, P. A.
1960. Effect of temperature and salinity on the oxygen consumption of two intertidal crabs. Biol. Bull. (Woods Hole) 118:215-249.

EGUSA, S.
1961. Studies on the respiration of the "Kuruma" prawn, *Penaeus japonicus* Bate.—II Preliminary experiments on its oxygen consumption. Bull. Jpn. Soc. Sci. Fish. 27:650-659.

ELDRED, B., R. M. INGLE, K. D. WOODBURN, R. F. HUTTON, AND H. JONES.
1961. Biological observations on the commercial shrimp, *Penaeus duorarum* Burkenroad, in Florida waters. Fla. State Board Conserv., Mar. Lab., Prof. Pap. Ser. 3, 139 p.

FONTAINE, C. T., AND R. A. NEAL.
1971. Length-weight relations for three commercially important penaeid shrimp of the Gulf of Mexico. Trans. Am. Fish. Soc. 100:584-586.

FRY, F. E. J.
1957. The aquatic respiration of fish. *In* M. E. Brown (editor), The physiology of fish, Vol. 1, p. 1-63. Acad. Press, N.Y.

GEORGE, M. J.
1974. The food of the shrimp *Metapenaeus monoceros* (Fabricius) caught from the backwaters. Indian J. Fish. 21:495-500.

GIESE, A. C.
1968. Cell physiology. 3d ed. Saunders, Phila., 671 p.

GILES, J. H., AND G. ZAMORA.
1973. Cover as a factor in habitat selection by juvenile brown (*Penaeus aztecus*) and white (*P. setiferus*) shrimp. Trans. Am. Fish. Soc. 102:144-145.

GOSSELINK, J. G., AND C. J. KIRBY.
1974. Decomposition of salt marsh grass, *Spartina alterniflora* Loisel. Limnol. Oceangr. 19:825-832.

GREEN, F. A., JR., J. W. ANDERSON, S. R. PETROCELLI, B. J. PRESLEY, AND R. SIMS.
1976. Effect of mercury on the survival, respiration, and growth of postlarval white shrimp, *Penaeus setiferus*. Mar. Biol. (Berl.) 37:75-81.

GUNTER, G
1945. Studies on marine fishes of Texas. Publ. Inst. Mar. Sci., Univ. Tex. 1(1):1-190.
1950. Seasonal population changes and distributions as related to salinity, of certain invertebrates of the Texas coast, including the commercial shrimp. Publ. Inst. Mar. Sci., Univ. Tex. 1(2):7-51.

GUNTER, G., J. Y. CHRISTMAS, AND R. KILLEBREW.
1964. Some relations of salinity to population distributions of motile estuarine organisms, with special reference to penaeid shrimp. Ecology 45:181-185.

GUNTER, G., AND H. H. HILDEBRAND.
1954. The relations of total rainfall of the state and catch of the marine shrimp (*Penaeus setiferus*) in Texas waters. Bull. Mar. Sci. Gulf Caribb. 4:95-103.

HARRIS, L. E.
1966. Biological energy interrelationships and glossary of energy terms. Publ. 1411, Natl. Acad. Sci., Natl. Res. Counc., Wash., D.C., 35 p.

HOESE, H. D.
1960. Juvenile penaeid shrimp in the shallow Gulf of Mexico. Ecology 41:592-593.

HUGHES, D. A.
1972. On the endogenous control of tide-associated displacements of pink shrimp, *Penaeus duorarum* Burkenroad. Biol. Bull. (Woods Hole) 142:271-280.

IKEDA, T.
1970. Relationship between respiration rate and body size in marine plankton animals as a function of the temperature of habitat. Bull. Fac. Fish. Hokkaido Univ. 21:91-112.

JONES, R. R., JR.
1973. Utilization of Louisiana estuarine sediments as a source of nutrition for the brown shrimp, *Penaeus aztecus*. Ph.D. Thesis, Louisiana State Univ., Baton Rouge, 131 p.

KADER, H.A.
1962. Ionic influence on oxygen consumption in *Metapenaeus monoceros* Fabricius. J. Anim. Morphol. Physiol. 9:32-40.

KEYS, A. B.
1930. The measurement of the respiratory exchange of aquatic animals. Biol. Bull. (Woods Hole) 59:187-198.

KHLEBOVICH, V. V.
1968. Some peculiar features of the hydrochemical regime and the fauna of mesohaline waters. Mar. Biol. (Berl.) 2:47-49.

KINNE, O.
1964. The effects of temperature and salinity on marine and brackish water animals. II. Salinity and temperature salinity combinations. Oceanogr. Mar. Biol. Annu. Rev. 2:281-339.
1966. Physiological aspects of animal life in estuaries with special reference to salinity. Neth. J. Sea Res. 3:222-244.
1967. Physiology of estuarine organisms with special reference to salinity and temperature: general aspects: *In* G. H. Lauff (editor), Estuaries, p. 525-540. AAAS Publ. 83.

KUTTY, M. N.
1969. Oxygen consumption of the prawns *Penaeus indicus* H. Milne Edwards and *Penaeus semisulcatus* de Haan. FAO Fish. Rep. 57:957-969.

KUTTY, M. N., G. MURUGAPOOPATHY, AND T. S. KRISHNAN.
1971. Influence of salinity and temperature on the oxygen consumption in young juveniles of the Indian prawn *Penaeus indicus*. Mar. Biol. (Berl.) 11:125-131.

LOFTS, B.
1956. The effects of salinity changes on the respiratory rate of the prawn *Palaemonetes varians* (Leach). J. Exp. Biol. 33:730-736.

MCFARLAND, W. N., AND B. D. LEE.
1963. Osmotic and ionic concentrations of penaeidean shrimps of the Texas coast. Bull. Mar. Sci. Gulf Caribb. 13:391-417.

MILL, P. J.
1972. Respiration in the invertebrates. The MacMillan Press Ltd., Lond., 212 p.

MISTAKIDIS, M. N.
1957. The biology of *Pandalus montagui* Leach. Fish. Invest., Minist. Agric., Fish. Food (G.B.), Ser. II, 21(4), 52 p.

MOLLER, T. H., AND D. A. JONES.
1975. Locomotory rhythms and burrowing habits of *Penaeus semisulcatus* (de Haan) and *P. monodon* (Fabricius) (Crustacea: Penaeidae). J. Exp. Mar. Biol. Ecol. 18:61-77.

MORIARTY, D. J. W.
1977. Quantification of carbon, nitrogen and bacterial biomass in the food of some penaeid prawns. Aust. J. Mar. Freshwater Res. 28:113-118.

NATIONAL MARINE FISHERIES SERVICE.
1978. Fishery statistics of the United States 1975. Natl. Mar. Fish. Serv., Stat. Dig. 69, 418 p.

NELSON, S. G., H. W. LI, AND A. W. KNIGHT.
1977. Calorie, carbon and nitrogen metabolism of juvenile *Macrobrachium rosenbergii* (De Man) (Crustacea, Palaemonidae) with regard to trophic position. Comp. Biochem. Physiol. 58A:319-327.

NOSE, T.
1964. Protein digestibility of several test diets on cray and prawn fish. [In Jpn., Engl. synop.] Bull. Freshwater Fish. Res. Lab. (Tokyo) 14:23-28.

PANIKKAR, N. K.
1951. Physiological aspects of adaptation to estuarine conditions. Proc. Indo-Pac. Fish. Counc. 2:168-175.
1968. Osmotic behaviour of shrimps and prawns in relation to their biology and culture. FAO Fish. Rep. 57:527-538.

PARKER, J. C.
1970. Distribution of juvenile brown shrimp (*Penaeus aztecus* Ives) in Galveston Bay, Texas, as related to certain hydrographic features and salinity. Publ. Inst. Mar. Sci., Univ. Tex. 15:1-12.

PASSANO, L. M.
1960. Molting and its control. *In* T. H. Waterman (editor), The physiology of Crustacea, Vol. 1, p. 473-536. Acad. Press, N.Y.

PÉREZ FARFANTE, I.
1969. Western Atlantic shrimps of the genus *Penaeus*. U.S. Fish Wildl. Serv., Fish. Bull. 67:461-591.

PROSSER, C. L.
1973. Oxygen: respiration and metabolism. *In* C. L. Prosser (editor), Comparative animal physiology, 3d ed., p. 165-211. Saunders, Phila.

PROSSER, C. L., AND F. A. BROWN, JR.
1961. Comparative animal physiology. 2d ed. Saunders, Phila., 688 p.

QASIM, S. Z., AND D. C. V. EASTERSON.
1974. Energy conversion in the shrimp, *Metapenaeus monoceros* (Fabricius), fed on detritus. Indian J. Mar. Sci. 3:131-134.

QASIM, S. Z., AND V. N. SANKARANARAYANAN.
1972. Organic detritus of a tropical estuary. Mar. Biol. (Berl.) 15:193-199.

RACEK, A. A.
1959. Prawn investigations in eastern Australia. N.S.W. State Fish., Res. Bull. 6, 57 p.

RAO, K. P.
1958. Oxygen consumption as a function of size and salinity in *Metapenaeus monoceros* Fab. from marine and brackish-water environments. J. Exp. Biol. 35:307-313.

RINGO, R. D.
1965. Dispersion and growth of young brown shrimp. *In* Biological laboratory, Galveston, Tex., fishery research for the year ending June 30, 1964, p. 68-70. U.S. Fish Wildl. Serv., Circ. 230.

ROEDEL, P. M.
1973. Shrimp '73—A billion dollar business. Mar. Fish. Rev. 35(3-4):1-2.

ROSE, C. D., A. H. HARRIS, AND B. WILSON.
1975. Extensive culture of penaeid shrimp in Louisiana salt-marsh impoundments. Trans. Am. Fish. Soc. 104:296-307.

ST. AMANT, L. S., J. G. BROOM, AND T. B. FORD.
1966. Studies of the brown shrimp, *Penaeus aztecus*, in Barataria Bay, Louisiana, 1962-1965. Proc. Gulf Caribb. Fish. Inst., 18th Annu. Sess., p. 1-17.

SCHOLANDER, P. F., W. FLAGG, V. WALTERS, AND L. IRVING.
1953. Climatic adaptation in arctic and tropical poikilotherms. Physiol. Zool. 26:67-92.

SCHWABE, E.
1933. Über die Osmoregulation verschiedener Krebse (Malacostracen). Z. vgl. Physiol. 19:183-236.

SICK, L. V., D. WHITE, AND G. BAPTIST.
1973. The effect of duration of feeding, amount of food, light intensity, and animal size on rate of ingestion of pelleted food by juvenile penaeid shrimp. Prog. Fish-Cult. 35:22-26.

SNEDECOR, G. W., AND W. G. COCHRAN.
1967. Statistical methods. 6th ed. Iowa State Univ. Press, Ames, 593 p.

STEED, D. L., AND B. J. COPELAND.
1967. Metabolic responses of some estuarine organisms to an industrial effluent. Publ. Inst. Mar. Sci., Univ. Tex. 12:143-159.

STEEL, R. G. D., AND J. H. TORRIE.
1960. Principles and procedures of statistics with special reference to the biological sciences. McGraw-Hill, N.Y., 481 p.

SUBRAHMANYAM, C. B.
1962. Oxygen consumption in relation to body weight and oxygen tension in the prawn *Penaeus indicus* (Milne Edwards). Proc. Indian Acad. Sci. 55B:152-161.
1976. Tidal and diurnal rhythms of locomotory activity and oxygen consumption in the pink shrimp, *Penaeus duorarum*. Contrib. Mar. Sci. 20:123-132.

VENKATARAMIAH, A., G. J. LAKSHMI, AND G. GUNTER.
1975. A review of the effects of some environmental and nutritional factors on brown shrimp, *Penaeus aztecus* Ives in laboratory cultures. 10th Eur. Symp. Mar. Biol., p. 523-547.

WATERMAN, T. H. (editor)
1960. The physiology of Crustacea, Vol. 1, Metabolism and growth. Acad. Press, N.Y., 670 p.

WEERASINGHE, M., AND K. D. ARUDPRAGASAM.
1967. The effect of salinity changes on the heart rate and oxygen consumption in *Penaeus indicus* (Milne Edwards). (Abstr.) Ceylon Assoc. Adv. Sci., Proc. 23d Annu. Sess., p. 51.

WEYMOUTH, F. W., M. J. LINDNER, AND W. W. ANDERSON.
1933. Preliminary report on the life history of the common shrimp, *Penaeus setiferus* (Linn.). Bull. [U.S.] Bur. Fish. 48:1-26.

WHEELER, J. F. G.
1937. Further observations on lunar periodicity. J. Linn. Soc. Lond. Zool. 40:325-345.

WICKHAM, D. A.
1967. Observations on the activity patterns in juveniles of the pink shrimp, *Penaeus duorarum*. Bull. Mar. Sci. 17:769-786.

WILLIAMS, A. B.
1955. A contribution to the life histories of commercial shrimps (Penaeidae) in North Carolina. Bull. Mar. Sci. Gulf Caribb. 5:116-146.
1958. Substrates as a factor in shrimp distribution. Limnol. Oceanogr. 3:283-290.
1960. The influence of temperature on osmotic regulation in two species of estuarine shrimps (*Penaeus*). Biol. Bull. (Woods Hole) 119:560-571.
1965. Marine decapod crustaceans of the Carolinas. U.S. Fish Wildl. Serv., Fish. Bull. 65:1-298.

WOLVEKAMP, H. P., AND T. H. WATERMAN.
1960. Respiration. *In* T. H. Waterman (editor), The physiology of Crustacea, Vol. 1, p. 35-100. Acad. Press, N.Y.

ZEIN-ELDIN, Z. P.
1963. Effect of salinity on growth of postlarval penaeid shrimp. Biol. Bull. (Woods Hole) 125:188-196.

ZEIN-ELDIN, Z. P., AND D. V. ALDRICH.
1965. Growth and survival of postlarval *Penaeus aztecus* under controlled conditions of temperature and salinity. Biol. Bull. (Woods Hole) 129:199-216.

ZEIN-ELDIN, Z. P., AND G. W. GRIFFITH.
1969. An appraisal of the effects of salinity and temperature on growth and survival of postlarval penaeids. FAO Fish. Rep. 57:1015-1026.

ZEIN-ELDIN, Z. P., AND E. F. KLIMA.
1965. Effects of injected biological stains on oxygen uptake by shrimp. Trans. Am. Fish. Soc. 94:277-278.

ZEUTHEN, E.
1947. Body size and metabolic rate in the animal kingdom with special regard to the marine micro-fauna. C. R. Trav. Lab. Carlsberg, Ser. Chim. 26:17-161.

DIEL AND SEASONAL VARIATION IN ABUNDANCE AND DIVERSITY OF SHALLOW-WATER FISH POPULATIONS IN MORRO BAY, CALIFORNIA

MICHAEL H. HORN[1]

ABSTRACT

More than 11,000 fishes weighing over 197 kg and representing 21 species were caught in bag seine hauls taken at quarterly periods (November 1974, May and August 1975, February 1976) in the southeastern section of Morro Bay. During each sampling period, nine seine hauls were completed, one at each 3-hour interval over a 24-hour cycle. *Atherinops affinis*, *Cymatogaster aggregata*, and *Leptocottus armatus* accounted for 82% of the individuals collected, and *A. affinis*, *C. aggregata*, and *Mustelus californicus* constituted 84% of the biomass obtained. Larger numbers of individuals and greater biomass were collected in night hauls, but nearly equal numbers of species were captured during the day and night. The largest number of species and individuals and greatest biomass were obtained in May, a period of high reproductive activity, whereas the smallest values of these three parameters were recorded in August. Diversity (H') for numbers peaked in May (1.56) but reached a maximum for biomass in November (1.91). Lowest diversity for both numbers (0.86) and biomass (0.79) was recorded in February. Total diversity was 1.63 for numbers and 1.59 for biomass. Wide ranging similarity values (PS) between consecutive sampling periods for numbers (24-64%) and biomass (21-76%) demonstrated the marked seasonality of the shallow-water fish populations of the bay and primarily reflected the fluctuations in numbers or biomass of the four most abundant species (above).

The pattern of total diversity and seasonal similarity for Morro Bay fishes was consistent with a recent model that utilizes diversity and similarity indices together as measures of environmental quality. Analysis of data from three other localities indicated that the model has the potential for application in a variety of temperate bay-estuarine habitats.

Morro Bay (Figure 1), an estuary located on the central California coast (lat. 35°20′ N), is one of the largest and least altered coastal wetlands in California and a critically important aquatic habitat. It supports abundant invertebrate populations and is an integral part of the Pacific flyway for migratory, water-associated birds (Gerdes et al. 1974). The bay is the site of rookeries for two species of herons, and the two endangered bird species, California least tern and peregrine falcon, utilize the resources of the bay. Steelhead occur in the tributary streams and a sizeable sport fishery exists in the bay. Although more than 60 species of fishes are known to occur in Morro Bay (Fierstine et al. 1973), little is known of the dynamics and organization of the fish communities. This lack of information provided the impetus for the present study.

The main purpose of the study was to assess in terms of abundance, diversity, and species composition, the diel (24 h) and seasonal variation of the fish community occurring in the shallow waters of the bay. In addition, the investigation was designed to provide a preliminary test in Morro Bay of the relationship proposed by Haedrich (1975) that indices of diversity (measuring species richness and equitability) and similarity (measuring seasonal composition and succession) as community parameters can be used together as indicators of environmental quality of temperate bays and estuaries. Based on trawl collections of fishes in nine Massachusetts estuaries and embayments, Haedrich (1975) showed that in habitats of low annual (or total) diversity little seasonal change is reflected in high similarity from season to season whereas in locations of high annual diversity lower similarity indicates a greater degree of seasonal change. Low diversities characterized areas of high pollution and higher diversities those of lesser pollution. Because of the reportedly low levels of environmental stress (including human-induced pollution) in Morro Bay (Gerdes et al. 1974), the expected outcome of the present study was that total diversity would be relatively high and similarity between seasons relatively low or show a wide range of values. Comparisons of total diversity and seasonal similarity were made between Morro Bay samples and bag seine collec-

[1]Department of Biology, California State University, Fullerton, CA 92634.

Manuscript accepted December 1979.
FISHERY BULLETIN: VOL. 78, NO. 3, 1980.

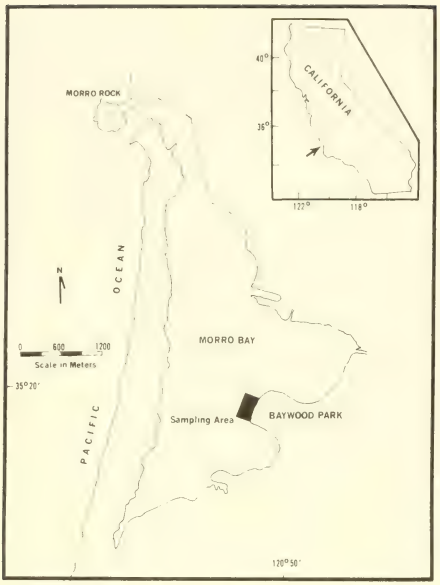


FIGURE 1.—Morro Bay, Calif. Shaded rectangle is the sampling area.

tions taken in three other California bay-estuarine habitats with similar ichthyofaunas.

THE STUDY AREA

Morro Bay is characterized by expansive tidal flats, central channels, and extensive eelgrass beds. During spring low tides, the bay is essentially reduced to a series of channels. Although two creeks empty into the bay, salinities are relatively uniform and approach those of the sea, making the bay more of a marine lagoon than a true estuary.

The study was conducted during quarterly periods (November 1974, May and August 1975, February 1976) in the shallow mudflat and channel area of the southeastern section of Morro Bay adjacent to Baywood Park (Figure 1). The substrate of the area was characterized by a relatively uniform mud-sand material, a large percentage of which was covered mainly by eelgrass, *Zostera marina*, and also a red alga, *Gracilaria* sp., and a green alga, *Ulva* sp. Water depth over the study area was as great as 2 m during high tide periods. Water temperature and salinity were recorded at 30 cm depth at the time each fish sample was taken. Temperatures ($\bar{x} \pm 1$ SD, $n = 9$) were 13.7°±1.4° C in February, 17.9°±0.5° C in May, 19.6°±2.9° C in August, and 11.8°±1.9° C in November. Salinity values were 30.9±0.7‰ in February, 30.0±0.8‰ in May, 31.1±1.0‰ in August, and 31.8±1.7‰ in November. Tidal ranges during the 24-h sampling periods varied from 1.0 m (3.3 ft) in May 1975 to 2.2 m (7.3 ft) in February 1976.

METHODS

Fish sampling was performed with the use of a seine 3 m deep by 29.2 m long with a 2.2 × 2.2 × 2.2 m bag of 6 mm mesh size. The seine was set parallel to the beach from a 3 m skiff and hauled to shore with polypropylene lines. The distance the seine was set from the water's edge was 60 m except at extreme low tides when there was water only in the channels. At these times (the tows at 1500 h and 1800 h in February), successive hauls covering small areas were made until the total area sampled was approximately equal to that of single hauls at higher tide periods. Samples were taken at randomly selected intervals along a 400 m stretch of shore. The total sampling area was approximately 2.4 ha (0.4-0.5% of the total area of the bay) and each seine haul covered about 0.18 ha. Based on visual surveys, this stretch of inshore habitat was typical (in terms of substrate, depth, and position relative to the mouth and main channel) of the rather uniform shallow-water conditions in the bay.

During each of the four sampling periods, seine hauls were made at 3-h intervals over a 24-h cycle for a total of nine samples per visit. For day-night comparisons, the second of the two 0900-h samples was not included each period so that equal numbers of day and night samples (four) were compared. All fishes captured, or aliquots of the largest catches of abundant species, were identified and sorted, and their standard lengths (SL) and weights recorded.

The Shannon-Wiener information function H' was calculated as a measure of diversity in which

$$H' = -\sum_{i=1}^{s} P_i \log P_i$$

where P_i is the proportion of individuals (or

biomass) in the ith species. Calculations were based on the use of natural logs ($\log_e$).

The degree of specific change between samples from one period to the next was calculated using the percentage similarity index (PS) developed by Whittaker and Fairbanks (1958). Percentage similarity ranges from 0, when two samples contain no species in common, to 100, when the two samples are identical in both species composition and relative abundance. The index is calculated as

$$PS = 100\,(1.0 - 0.5 \sum \left| P_{ia} - P_{ib} \right|)$$

where P_{ia} is the proportion of individuals (biomass) in the ith species of sample a and P_{ib} the same for sample b. The basic data are the same as are required for the calculation of H', i.e., the number or biomass of individuals in each species of the sample.

RESULTS

A total of 11,627 fishes weighing 197,747 g were captured in 36 seine hauls taken during the four sampling periods (Table 1). Of the 21 species collected, three species, *Atherinops affinis*, *Cymatogaster aggregata*, and *Leptocottus armatus*, composed almost 82% of the total individuals. A fourth species, *Engraulis mordax*, contributed 11.2% of the total. *Mustelus californicus*, *A. affinis*, and *C. aggregata*, accounted for nearly 84% of the biomass collected. *Leptocottus armatus* contributed an additional 7% to the total biomass.

For the four sampling periods taken together,

TABLE 1.—Number of individuals and biomass of fish species collected by beach seine in Morro Bay during four 24-h periods from November 1974 to February 1976. The proportion that each species contributed to total numbers and biomass of each sampling period is expressed as a percentage (%). (Species ranked according to total numbers for the four periods.)

	February 1976				May 1975				August 1975				November 1974				Totals			
	Individuals		Biomass		Individuals		Biomass		Individuals		Biomass		Individuals		Biomass		Individuals		Biomass	
Species	No.	%	g	%	No.	%	g	%	No.	%	g	%	No.	%	g	%	No.	%	g	%
Atherinops affinis	351	16.0	3,996	8.0	998	23.4	40,940	41.2	309	14.2	9,099	41.1	1,960	65.5	7,856	29.7	3,618	31.1	61,891	31.3
Cymatogaster aggregata	—	—	—	—	1,498	35.1	41,049	41.3	1,530	70.4	6,793	30.6	67	2.2	575	2.2	3,095	26.6	48,417	24.5
Leptocottus armatus	1,668	76.2	2,063	4.1	644	15.1	3,649	3.7	272	12.5	3,725	16.8	196	6.5	4,444	16.8	2,780	23.9	13,881	7.0
Engraulis mordax	—	—	—	—	909	21.3	1,532	1.5	2	0.09	3	—	397	13.3	280	1.1	1,308	11.2	1,815	0.9
Fundulus parvipinnis	25	1.1	50	0.1	1	—	10	—	—	—	—	—	229	7.6	728	2.7	255	2.2	788	0.4
Syngnathus leptorhynchus	18	0.8	24	0.05	35	0.8	200	0.2	18	0.8	111	0.5	94	3.1	850	3.2	165	1.4	1,185	0.6
Quietula y-cauda	26	1.2	49	0.1	64	1.5	158	0.2	27	1.2	94	0.4	2	0.1	2	—	119	1.0	303	0.2
Micrometrus minimus	7	0.3	152	0.3	77	1.8	152	0.2	—	—	—	—	6	0.2	149	0.6	90	0.8	453	0.2
Lepidogobius lepidus	43	2.0	6	0.01	—	—	—	—	—	—	—	—	1	—	4	—	44	0.4	10	—
Embiotoca jacksoni	—	—	—	—	11	0.3	171	0.2	9	0.4	340	1.5	17	0.6	1,238	4.7	37	0.3	1,749	0.9
Atherinopsis californiensis	25	1.1	3,659	7.3	1	—	280	0.3	1	0.05	230	1.0	5	0.2	1,296	4.9	32	0.3	5,465	2.8
Mustelus californicus	19	0.9	39,463	79.3	7	0.2	8,322	8.4	—	—	—	—	3	0.1	7,296	27.5	29	0.3	55,081	27.9
Damalichthys vacca	1	0.05	240	0.5	19	0.4	2,390	2.4	—	—	—	—	2	0.1	450	1.7	22	0.2	3,080	1.6
Clupea harengus	1	0.05	88	0.2	—	—	—	—	—	—	—	—	13	0.4	1,276	4.8	14	0.1	1,364	0.7
Clevelandia ios	2	0.1	2	—	2	—	—	—	1	0.05	2	—	1			—	6	0.1	4	—
Hyperprosopon argenteum	—	—	—	—	3	0.1	121	—	—	—	—	—	1		50	0.2	4	—	171	0.1
Myliobatis californica	—	—	—	—	—	—	—	—	3	0.1	1,760	7.9	—	—	—	—	3	—	1,760	0.9
Citharichthys stigmaeus	3	0.1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	3	—	1	—
Hypsopsetta guttulata	—	—	—	—	1	—	320	0.3	—	—	—	—	—	—	—	—	1	—	320	0.2
Platichthys stellatus	—	—	—	—	—	—	—	—	1	0.05	8	—	—	—	—	—	1	—	8	—
Sebastes sp.	—	—	—	—	1	—	1	—	—	—	—	—	—	—	—	—	1	—	1	—
Totals	2,189		49,793		4,271		99,295		2,173		22,165		2,994		26,494		11,627		197,747	
Total species	13				16				11				16				21			

nearly equal numbers of species were collected during the day (14) and night (15) (Table 2); however, significantly greater numbers of individuals and biomass were obtained during the night (Table 3). The *PS* value between day and night samples was higher for numbers (68.5%) than for biomass (43.3%). In February, nearly equal numbers of species were collected during the day (9) and night (10). Greater numbers of individuals were collected at night but the difference was not significant. Even though the total biomass obtained during the day in February was greater than that at night, the night samples were more frequently and significantly larger based on paired day-night abundances of each species using the Wilcoxon signed-ranks test (Table 3). The discrepancy was due to the exceptionally large daytime contribution (34,246 g) of *M. californicus* compared with its much smaller contribution (3,402 g) to the night samples. The *PS* value between day and night samples was much higher for numbers (83.3%) than for biomass (40.5%). In May, more species were collected at night (14) than during the day (8). Greater numbers of individuals and biomass were obtained at night but the difference was significant only for numbers. The *PS* value between day and night samples was higher for numbers (60.3%) than for biomass (42.0%). In August, nearly equal numbers of species were collected during the day (eight) and night (seven).

TABLE 2.—Relative numbers and biomass (expressed as percentage) of fish species collected in four daytime (0900-1800 h) and four nighttime (2100-0600 h) seine hauls for each sampling period and the total collection in Morro Bay. (Species ranking as in Table 1.)

	February 1976				May 1975				August 1975			
	No. individuals		Biomass		No. individuals		Biomass		No. individuals		Biomass	
Species	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night
Atherinops affinis	19.8	7.6	1.1	31.8	33.1	15.9	78.5	26.2	33.0	19.7	26.6	53.3
Cymatogaster aggregata	—	—	—	—	14.1	49.5	11.2	56.6	50.5	61.2	9.3	28.1
Leptocottus armatus	66.8	88.3	0.7	16.8	14.7	14.5	4.6	3.4	8.0	16.7	7.0	17.9
Engraulis mordax	—	—	—	—	34.7	13.4	3.8	0.8	1.0	—	0.1	—
Fundulus parvipinnis	0.5	0.8	—	0.4	—	—	—	—	—	—	—	—
Syngnathus leptorhynchus	0.8	0.1	—	0.2	1.0	0.8	0.5	0.1	5.0	0.3	2.0	0.1
Quietula y-cauda	1.0	1.4	—	0.4	2.0	1.3	0.3	0.1	1.0	1.9	0.1	0.6
Micrometrus minimus	1.5	0.1	0.4	0.1	0.3	2.8	0.1	0.2	—	—	—	—
Lepidogobius lepidus	—	—	—	—	—	—	—	—	—	—	—	—
Embiotoca jacksoni	—	—	—	—	—	0.5	—	0.3	—	—	—	—
Atherinopsis californiensis	4.5	0.4	5.5	14.0	0.1	—	1.0	—	1.0	—	6.4	—
Mustelus californicus	4.0	0.1	92.3	33.1	—	0.2	—	7.8	—	—	—	—
Damalichthys vacca	—	0.1	—	2.3	—	0.7	—	3.8	—	—	—	—
Clupea harengus	—	0.1	—	0.9	—	—	—	—	—	—	—	—
Clevelandia ios	—	—	—	—	—	0.1	—	—	—	0.1	—	—
Hyperprosopon argenteum	—	—	—	—	—	0.1	—	0.2	—	—	—	—
Myliobatis californica	—	—	—	—	—	—	—	—	2.0	—	48.6	—
Citharichthys stigmaeus	0.8	—	—	—	—	—	—	—	—	—	—	—
Hypsopsetta guttulata	—	—	—	—	—	0.1	—	0.5	—	—	—	—
Platichthys stellatus	—	—	—	—	—	—	—	—	—	0.1	—	0.1
Sebastes sp.	—	—	—	—	—	0.1	—	—	—	—	—	—
Totals	398	1,540	37,120	10,272	1,751	2,209	27,435	62,706	200	1,149	3,622	14,111
Total species	9	10			8	14			8	7		

TABLE 2.—*Continued.*

	November 1974				Totals			
	No. Individuals		Biomass		No. individuals		Biomass	
Species	Day	Night	Day	Night	Day	Night	Day	Night
Atherinops affinis	65.0	66.4	34.4	28.2	44.3	25.3	33.8	30.9
Cymatogaster aggregata	1.0	3.9	1.3	3.8	9.3	29.7	4.4	40.7
Leptocottus armatus	4.2	6.7	14.3	15.2	15.6	31.5	4.5	8.2
Engraulis mordax	25.7	0.2	2.0	0.1	25.8	4.8	1.6	0.5
Fundulus parvipinnis	1.6	14.8	0.6	5.6	0.7	3.4	0.1	0.7
Syngnathus leptorhynchus	1.3	5.6	1.1	6.5	1.3	1.8	0.4	0.8
Quietula y-cauda	—	0.2	—	—	1.0	1.2	0.1	0.2
Micrometrus minimus	0.3	0.1	1.1	—	0.4	1.0	0.4	0.1
Lepidogobius lepidus	—	0.1	—	—	—	—	—	—
Embiotoca jacksoni	0.7	0.5	5.0	5.4	0.3	0.3	0.8	0.8
Atherinopsis californiensis	0.1	0.2	3.3	8.0	0.6	0.1	3.7	2.4
Mustelus californicus	0.1	0.1	35.0	12.7	0.4	0.1	47.8	9.9
Damalichthys vacca	0.1	0.1	1.8	2.0	—	0.3	0.3	2.9
Clupea harengus	—	1.0	—	11.8	—	0.2	—	1.4
Clevelandia ios	0.1	—	—	—	0.1	0.1	—	—
Hyperprosopon argenteum	—	0.1	—	0.5	—	0.1	—	0.2
Myliobatis californica	—	—	—	—	0.1	—	2.2	—
Citharichthys stigmaeus	—	—	—	—	0.1	—	—	—
Hypsopsetta guttulata	—	—	—	—	—	—	—	0.3
Platichthys stellatus	—	—	—	—	—	—	—	—
Sebastes sp.	—	—	—	—	—	—	—	—
Totals	1,535	1,320	13,038	10,791	3,884	6,218	81,215	97,880
Total species	12	15			14	15		

TABLE 3.—Day and night fish samples in terms of numbers of individuals and biomass for each sampling period and the total collection in Morro Bay. Percentage similarity (*PS*) is explained in the text. "Difference" column indicates whether day samples were significantly (S) or not significantly (NS) different from night samples based on paired percentage values for each species (Table 2) (Wilcoxon signed-ranks test for paired values, $P = 0.05$, two-tailed).

	No. of individuals				Biomass			
Sampling period	Day	Night	Percentage similarity	Difference	Day	Night	Percentage similarity	Difference
February 1976	398	1,540	83.3	NS	37,120	10,272	40.5	S (night>day)
May 1975	1,751	2,209	60.3	S (night>day)	27,435	62,706	42.0	NS
August 1975	200	1,149	78.8	NS	3,622	14,111	43.0	NS
November 1974	1,535	1,320	74.1	S (night>day)	13,038	10,791	68.5	S (night>day)
Totals	3,884	6,218	68.5	S (night>day)	81,215	97,880	54.3	S (night>day)

Greater numbers and biomass were obtained at night but the difference was not significant in either case. The *PS* value between day and night samples was much higher for numbers (78.8%) than for biomass (43.0%). In November, more species were collected at night (15) than during the day (12). Even though the total number of individuals and total biomass obtained during the day were greater than the totals at night, the night samples in both cases were more frequently and significantly larger based on paired day-night abundances of each species using the Wilcoxon signed-ranks test (Table 3). The discrepancy for individuals was primarily due to a relatively large daytime contribution (394 individuals) of *E. mordax* compared with its much smaller number (3 individuals) in the night samples. The inconsistency for biomass was mainly due to the large daytime contribution (4,560 g) of *M. californicus* compared with its smaller contribution (1,368 g) to the night totals.

Seven species, *A. affinis, C. aggregata, L. armatus, E. mordax, Fundulus parvipinnis, Syngnathus leptorhynchus*, and *Quietula y-cauda*, were captured at least once in each of the 3-h sampling intervals of the four periods. No common species was collected either only during the day or only at night. Among the uncommon species, *Myliobatis californica* and *Citharichthys stigmaeus* were captured only during the day whereas *Clupea harengus, Hyperprosopon argenteum, Hypsopsetta guttulata, Platichthys stellatus*, and *Sebastes* sp. were obtained only at night (Table 2).

Marked changes in numbers, biomass, and diversity occurred between sampling periods although only four species, *A. affinis, Cymatogaster aggregata, L. armatus*, and *Mustelus californicus*, were, in different combinations, the most abundant (numbers or biomass) fishes in the samples (Table 1; Figure 2). Numbers of individuals and biomass both reached highest levels in May and lowest levels in August. Diversity H' on numbers

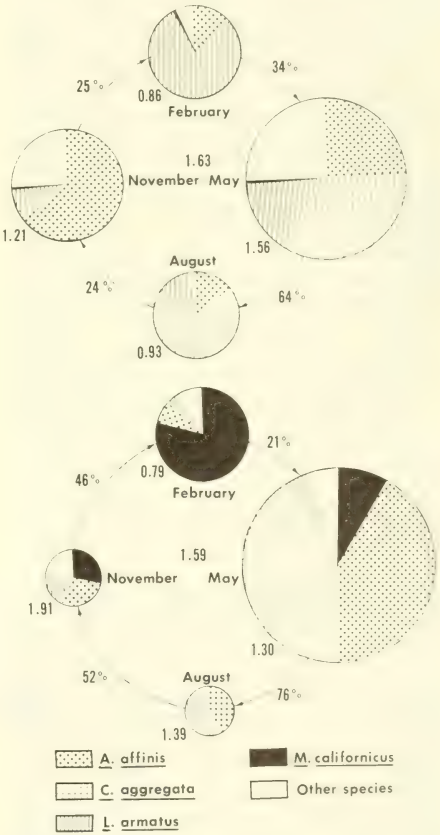


FIGURE 2.—Quarterly data on fish numbers (upper) and biomass (lower) in the Baywood Park section of Morro Bay. Total diversity is given by H' in the center of each cycle. The area of each circle is proportional to the sample size, the number to the lower left of each circle is the quarterly diversity H', and the number on the connecting arrow is the percentage similarity between months. Sampling dates are February 1976, May and August 1975, and November 1974.

was highest in May and lowest in February, whereas H' on biomass was greatest in November but also lowest in February. The *PS* levels for both numbers and biomass were highest between May and August. Lowest *PS* values were obtained for numbers between August and November and for biomass between February and May. Total diversity H' on numbers was similar to that for biomass.

Of the four common species in the samples, *A. affinis* was the most abundant species, composing 31% of both total individuals and biomass (Table 1). For the total collection, significantly more individuals and biomass of *A. affinis* were captured at night than during the day; however, for quarterly periods, a significant day-night difference was recorded only for numbers (night>day) in August (Table 4). Although somewhat larger individuals were commonly obtained in night compared with day samples, the differences were not significant for any collecting period (Table 4). In February, *A. affinis* were bimodal in length frequency (Figure 3), intermediate in mean size (Figure 4), and obtained in small numbers and the smallest biomass. The contribution of *A. affinis* to the total February catch was relatively minor for both numbers (16% of total) and biomass (8%). In May, the largest fish of the four periods were captured and in relatively high numbers. The biomass obtained was the greatest of the study for the species composing >41% of the total May sample. In August, the fish were strongly bimodal in length frequency and smaller in mean size. Numbers reached their lowest level and biomass declined but nevertheless made up >41% of the total August sample. In November, the smallest fish of the study were captured, but they occurred in the greatest numbers and composed >65% of the total November sample. The biomass value, because of the smaller fish, was lower than that for August.

Cymatogaster aggregata, even though absent from February samples, was the second most abundant species composing >26% of total numbers and >24% of total biomass (Table 1). In all sampling periods that *C. aggregata* was captured, larger numbers and greater biomass of the species were collected at night than during the day; however, the differences were significant only in May (Table 4). Although somewhat larger individuals were, in most cases, captured in night compared with day samples, the difference was significant only during May (Table 4). In May, the largest fish of the study were collected (Figure 4) but a wide size range was also represented (Figure 3). Numbers were relatively high and the biomass obtained was the greatest of the study for the species composing >41% of the total May sample. In August, the smallest fish of the study were collected. Biomass declined but numbers increased relative to the previous period and made up >70% of the total August sample. Slightly larger fish were collected in November but numbers and biomass reached low levels, each composing only about 2% of the totals.

Leptocottus armatus was the third most abundant species, composing almost 24% of total numbers but only 7% of total biomass (Table 1). In all sampling periods, larger numbers and greater

TABLE 4.—Number of individuals, biomass, and mean weight of the three most abundant fish species for each sampling period and the total collection in Morro Bay. "Difference" line indicates whether day (D) samples were significantly (S) or not significantly (NS) different from night (N) samples based on four ranked samples from each day and each night period for each species (Mann-Whitney U-test, $P \leq 0.05$, two-tailed).

	Atherinops affinis			*Cymatogaster aggregata*			*Leptocottus armatus*		
Item	Individuals (no.)	Biomass (g)	Mean weight (g)	Individuals (no.)	Biomass (g)	Mean weight (g)	Individuals (no.)	Biomass (g)	Mean weight (g)
February 1976:									
Day	79	412	5.2	—	—	—	266	265	1.0
Night	118	3,264	27.7	—	—	—	1,360	1,728	1.3
Difference	NS	NS	NS				S (N>D)	S (N>D)	NS
May 1975:									
Day	580	21,548	37.2	247	3,069	12.4	258	1,259	4.9
Night	351	16,441	46.8	1,094	35,480	32.4	321	2,155	6.7
Difference	NS	NS	NS	S (N>D)	S (N>D)	S (N>D)	NS	NS	NS
August 1975:									
Day	66	964	14.6	101	337	3.3	16	255	15.9
Night	226	7,520	33.3	703	3,959	5.6	192	2,520	13.1
Difference	S (N>D)	NS	NS	NS	NS	NS	NS	NS	NS
November 1974:									
Day	997	4,489	4.5	15	163	10.9	65	1,869	28.8
Night	877	3,045	3.5	52	412	7.9	88	1,645	18.7
Difference	NS	NS	NS	NS	NS	NS	NS	NS	NS
Totals:									
Day	1,722	27,413	15.9	363	3,569	9.8	605	3,648	6.0
Night	1,572	30,270	19.3	1,849	39,851	21.6	1,961	8,048	4.1
Difference	S (N>D)	S (N>D)	NS	NS	NS	NS	S (N>D)	S (N>D)	NS

FIGURE 3.—Length frequencies of the three most abundant fish species for the quarters sampled in Morro Bay. Sampling dates are February 1976, May and August 1975, and November 1974.

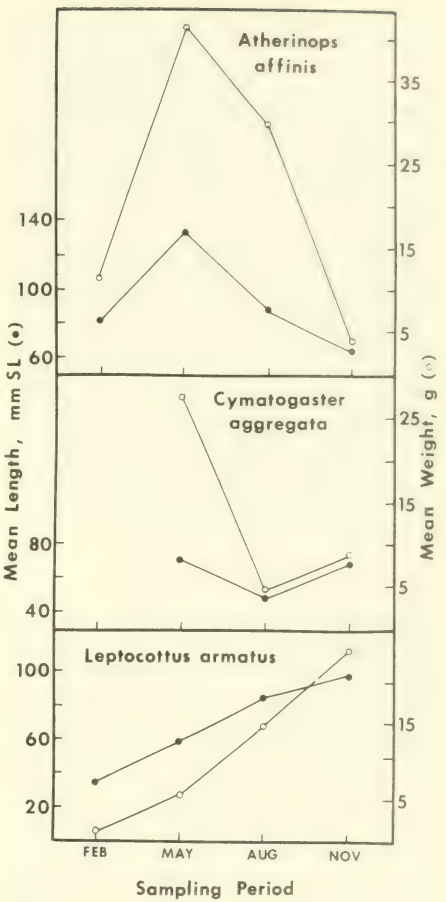


FIGURE 4.—Mean lengths (dots) and weights (circles) of the three most abundant fish species for the quarterly sampling periods in Morro Bay. Sampling dates are February 1976, May and August 1975, and November 1974.

biomass of *L. armatus* were collected at night than during the day; the differences were significant for the February sample and the total collection (Table 4). No significant differences in mean size were found between day and night samples; slightly larger individuals were captured at night in February and May whereas somewhat larger fish were collected during the day in August and November (Table 4). In February, the smallest fish of the study (Figures 3, 4) were collected in large numbers. The number of individuals composed >76% of the total sample; however, biomass contributed only about 4% of the total. In May, fish size and biomass increased whereas numbers de-

creased. This pattern continued through the August and November sampling periods and was in sharp contrast to that recorded for either *A. affinis* or *C. aggregata*. In August, a small number of relatively large *L. armatus* were collected. The corresponding biomass accounted for more than 16% of the total sample. In November, a small number of larger individuals were captured. The corresponding biomass made up >16% of the total sample.

Although only 29 individuals of a fourth species, *M. californicus*, were captured during the study, the fish ranked second in biomass and accounted for almost 28% of the weight of the total collection (Table 1). The largest number of *M. californicus* were caught in February when they were concentrated in the channels as a result of the spring low tide. The corresponding biomass accounted for >79% of the total February sample (Figure 2). Mean size was 834 mm total length and mean weight was 2,077 g. Too few specimens were collected to compare the abundance and mean size of individuals in day and night samples.

DISCUSSION

The results of this study indicate that the shallow-water fish populations of Morro Bay undergo both diel and seasonal variations in abundance (numbers and biomass), diversity, and species composition. A relatively small number of species (three) accounted for a large proportion (82%) of the total number of individuals collected. These findings are consistent with the results of several other studies of temperate bay-estuarine fish populations that have been reviewed by Allen and Horn (1975). A pattern that emerged from these studies was that at least 75% of the sampled fishes belonged to five or fewer species even though many more species were collected.

In terms of overall diel variation, more individuals and greater biomass were obtained in night samples but nearly equal numbers of species were collected during the day and night. Very few species, usually the rarer forms, were captured either only during the day or only at night.

Although surprisingly little is known concerning day-night differences in utilization of various habitats by fishes (McCleave and Fried 1975), most of the information that is available on trawl or seine samples in inshore waters indicate that greater catches, either of species, individuals, or biomass, are obtained at night (e.g., Hoese et al. 1968; Allen 1976; Livingston 1976). McCleave and Fried (1975) collected fewer total individuals at night and equal numbers of species day and night with a beach seine in a Maine tidal cove; however, they found that four numerically important species were either present only at night or more abundant at night.

Diurnal-nocturnal activity patterns and daytime gear avoidance, particularly by larger fish, are two factors among a complexity of circumstances that produce day-night differences in abundance and composition of net-caught fishes. Little is known about the first factor for bay-estuarine fishes although McCleave and Fried (1975) reviewed the diel patterns of a few inshore species. They and Hoese et al. (1968) both considered the second factor to be of importance in their respective studies. In my study, gear avoidance probably was one of the factors causing the generally smaller (numerically) daytime catches. However, size differences of day vs. night captured individuals of the three most abundant species were insignificant in almost all cases thus casting doubt on the assumption that the larger fish avoid the seine in the daytime. This reasoning is perhaps most relevant for *L. armatus*, the only nonschooling member of the three-species group.

Quarterly fluctuations in biomass (totals, diversity H', and *PS* values) were of greater magnitude than those for numbers, but both parameters expressed the seasonal dynamics of fish populations in the shallow waters of the bay. In February low numbers and biomass diversity but relatively high total biomass represented an early influx of prereproductive adults. The peak numbers and biomass reached in May corresponded to an abundance of *A. affinis* and *C. aggregata* of mature size (see species accounts below) as well as the presence of several other species in wide size ranges. Reduced numbers and biomass in August but high *PS* values for both numbers and biomass between May and August indicated that young-of-the-year fishes remained in the shallow waters while larger individuals migrated out of the sampling area. The large number of individuals and high biomass diversity recorded for November was the result of a relatively even distribution of biomass among juvenile fishes which continued to utilize the inshore areas late in the year.

Seasonal abundance and diversity were only partly attributable to variations in physical factors. Salinity was not an important factor because values were relatively high and varied little in the

sampling area, an indication of the marine character of the bay. Tidal ranges were smallest in May, the period of highest fish abundance, and largest in February, the month of lowest diversity. Temperature, the environmental factor most frequently recognized as having a major influence on temperate, shallow-water fish populations (e.g., Allen and Horn 1975; Subrahmanyam and Drake 1975; Wallace 1975; Hoff and Ibara 1977), did not consistently correspond to changes in abundance and diversity of Morro Bay fish populations: The largest increase in mean temperature (4° C) occurred between February and May, the transition period marked by the greatest increase in abundance and diversity. In contrast, the greatest decline in temperature between sampling periods (8° C from August to November) was accompanied by a substantial increase in abundance and diversity.

The life history patterns of the three most abundant species, *A. affinis, C. aggregata*, and *L. armatus*, serve not only to help clarify the seemingly conflicting responses to temperature of the fish populations but to illustrate the strategies of utilization of a bay-estuarine environment by inshore fishes. These patterns, recognized in previous studies, are discussed in turn below for each of the three species and related to the data I recorded in Morro Bay.

In his study of *A. affinis* in Newport Bay in southern California, Fronk (1969) recognized 3 age classes based on length frequencies (80-90 mm fork length in the first year; 120-130 mm by the second year; 150 mm after the third year) and found that spawning occurred from February to August (peak in May) when the fish were in their second and third years of life. These findings correspond to the seasonal length frequencies and abundance I recorded for *A. affinis* in Morrow Bay. In February, the bimodal size distribution included small numbers of both immature and larger individuals, some of which had mature gonads. May was marked by a high abundance of large fish, many of which released eggs and milt upon capture. The substrate of the sampling area apparently is an optimal spawning site since it is known (Frey 1971) that *A. affinis* attaches its eggs to eelgrass and low-growing algae such as *Gracilaria* sp. The egg masses were frequently found on the vegetation that was obtained in the seine hauls. By August, the number of small juveniles had increased but adult numbers had decreased. The overwhelming domination of the November catch by first (mainly) and second year fish is consistent with the apparent movement of postreproductive adults out of the shallow spawning areas that become nursery grounds for the juvenile fish.

In his study of *C. aggregata* in Anaheim Bay in southern California, Odenweller (1975) identified three age classes based on otolith rings and length frequencies. Fish in their first year ranged between 31 and 87 mm SL ($\bar{x}$ 57 mm), in their second year between 68 and 115 mm ($\bar{x}$ 88 mm) and in their third year between 81 and 117 mm ($\bar{x}$ 101 mm). *Cymatogaster aggregata* gives birth in the spring, primarily in May, according to Bane and Robinson (1970) and Odenweller (1975). Both Bane and Robinson (1970) and Allen (1976) found that in Newport Bay (southern California) the majority of adults migrate out of the bay after breeding in the spring leaving juveniles to utilize the area as a nursery ground. These adults apparently return to the bay to bear young the following spring. The seasonal abundance and size frequencies of *C. aggregata* in Morro Bay are in accord with the patterns found in the southern California bays and estuaries. The absence of the fish in February, its abundance in a wide size range in May and the presence of almost only small juveniles in August are indicative of the existence of the migratory breeding pattern in Morro Bay. The November catch, consisting of a small number of juveniles slightly larger than the August individuals, is further support for the existence of the pattern. Most of the young-of-the-year, which mature at or soon after birth (Bane and Robinson 1970), apparently moved out of the shallows after mating in the late summer or early fall.

According to studies carried out by Jones (1962) in Tomales Bay (near San Francisco) and San Francisco Bay and Tasto (1975) in Anaheim Bay (near Los Angeles), *L. armatus* is a winter spawner with the peak in January and February. Sexual maturity is reached near the end of the first year of life at approximately 120-150 mm SL for females and 110-120 mm SL for males. Tasto (1975) found that the Anaheim Bay population consisted almost entirely of juvenile fish and that postspawning mortality was apparently high, based on the absence of the older fish in the population, a sharp reduction in the catch per unit effort of adults during the breeding season and the capture of only two spent females. The data I obtained on *L. armatus* in Morro Bay are generally consistent with those of the two studies cited. Following the February sample, which was composed almost entirely of small juveniles, the frequency of

larger fish progressively increased through the successive quarterly periods so that in November the catch was made up of primarily large juveniles and secondarily of fish in the reported mature size range. Winter spawning was evident even though few adults were collected. The rarity of adults could have been due to at least four factors: 1) net avoidance by adults, 2) postspawning mortality by adults, 3) migration of adults out of the area after spawning, or 4) migration of young individuals into the area after spawning occurred elsewhere. Although the third factor has been discounted by Tasto (1975), all four possible causes deserve further investigation.

In terms of Haedrich's (1975) model for assessing the environmental quality of estuaries and embayments, Morro Bay can be classified as a relatively unspoiled habitat in that relatively high total diversity and a wide range of seasonal similarity values were recorded. It is instructive, however, to compare the Morro Bay data with those available for three southern California bay-estuarine habitats with similar ichthyofaunas: 1) Mugu Lagoon (lat. 34.1° N), 2) Colorado Lagoon (lat. 33.8° N), and 3) upper Newport Bay (lat. 33.6° N). Mugu Lagoon is a relatively unaltered habitat with diversity and similarity values comparable to those for Morro Bay whereas Colorado Lagoon and upper Newport Bay, two more highly perturbated sites, have lower diversity values yet wider ranging season-to-season similarity indices than Morro Bay or Mugu Lagoon (Table 5).

All four habitats are largely marine in character with salinities usually approaching those of the ocean. Upper Newport Bay is the most frequent exception in that during occasional years of heavy winter rainfall salinities are greatly reduced in the extreme upper portions of the habitat. Although generally considered to be a relatively unaltered estuary in southern California (Frey et al. 1970), upper Newport Bay, unlike Morro Bay, is subject to pollutant inflow from both urban and agricultural runoff and a high rate of sedimentation (with accompanying increased turbidity) during years of increased rainfall (e.g., Horn and Allen in press). Colorado Lagoon, the partially isolated upper arm of Alamitos Bay, receives pollutants and nutrients from street runoff and heavy recreational use especially during the summer months when eutrophic conditions usually develop (Allen and Horn 1975). The lower reaches of both Newport Bay and Alamitos Bay have been altered by extensive marina development and by modification of their openings to the sea. Mugu Lagoon is in a relatively undisturbed condition primarily because it has been for more than 30 yr under ownership of the U.S. Navy which restricts access to the area (MacDonald 1976). The fish faunas of these three environments are basically similar to that of Morro Bay with three of the five most abundant species in upper Newport Bay and Mugu Lagoon and four of the five most abundant species in Colorado Lagoon also in the top five in Morro Bay.

The sampling procedure (bag seine deployed from shore) and substrate conditions (varying mud to sand) were similar for the four habitats. Collections were made monthly in the locations other than Morro Bay; quarterly data were extracted for comparison with the Morro Bay values. The main difference in the collection of data among the four locations was the type of beach seine used. In Colorado Lagoon, as in Morro Bay, a 29.2 m seine with 6 mm mesh in the bag was used, whereas in Mugu Lagoon and upper Newport Bay a 15.2 m seine with 3 mm mesh in the bag was employed. The difference in effectiveness of the two types of seines is incompletely known but considered to be slight (M. H. Horn and L. G. Allen unpubl. data); moreover, the discrepancy is judged to be of minor importance since it does not parallel the diversity-similarity differences among the four ichthyofaunas (Table 5).

Quarterly data (February-November 1977) from bag seine samples of 29 species in Mugu Lagoon (Quammen[2]) yielded a total H' value of 1.52 and PS values ranging from 30 to 62% (Table 5). Thus,

TABLE 5.—Number of species (S), Shannon-Weiner diversity (H'), and season-to-season percentage similarity values (PS) based on quarterly bag seine collections of fishes in four bay-estuarine habitats in California. Environmental status is a qualitative assessment (see discussion section).

Bay-estuary	Location (latitude)	S	H	PS	Environmental status	Data source
Morro Bay	Central California (35.3° N)	21	1.63	24-64	Relatively unaltered	This study
Mugu Lagoon	Southern California (34.1° N)	29	1.52	30-62	Relatively unaltered	M. L. Quammen (unpubl. data)
Colorado Lagoon	Southern California (33.8° N)	16	0.75	2-57	Highly altered	Allen and Horn (1975)
Upper Newport Bay	Southern California (33.6° N)	23	0.66	13-96	Moderately altered	Horn and Allen (in press)

the diversity and similarity pattern for Mugu Lagoon is close to that for Morro Bay as would be expected for an unspoiled habitat. Data obtained during quarterly periods (February-November 1978) from bag seine collections of 23 species in upper Newport Bay (Horn and Allen in press) resulted in a total H' value of 0.66 and *PS* indices ranging from 13 to 96% (Table 5). Quarterly bag seine data (February-November 1973) for 16 species in Colorado Lagoon (Allen and Horn 1975) produced a total H' value of 0.75 and *PS* measures ranging from 2 to 57% (Table 5). According to the Haedrich (1975) model, the relatively low diversity values for upper Newport Bay and Colorado Lagoon should be accompanied by high similarity values and dominance of the community by one or a few species. However, a combination not explicitly recognized by Haedrich, that of low diversity and wide ranging seasonal similarity, is evident in these two habitats. Low H' values combined with variable *PS* values indicate a high seasonal abundance of one or a few species. This condition is realized in that in each case there was an extreme summer abundance of only one species—*A. affinis* in upper Newport Bay and *E. mordax* in Colorado Lagoon. In the most highly stressed habitat, low diversity, and a high relative abundance of a single species over the entire year (i.e., high seasonal similarity) would be predicted by the model. Thus, upper Newport Bay and Colorado Lagoon would be rated as intermediate in environmental quality. In general, Colorado Lagoon could be considered as the more highly perturbated of the two habitats (Table 5). The heavy rainfall of 1978, the year in which the upper Newport Bay data were collected, probably was a primary factor in producing the low diversity and divergent similarity values (Horn and Allen in press).

The use of the two indices in combination appears to have greater resolution and predictive strength than the use of only species diversity as an indicator of pollution, as has been proposed by Bechtel and Copeland (1970). Diversity H' provides information on species richness and equitability but not on species composition. The absolute replacement of one species by another, possibly a result of environmental alteration, would not be detected by a diversity measure nor would the seasonal succession of individual species. An index of similarity provides an indication of the magnitude and direction of seasonal dynamics.

The diversity-similarity approach holds promise as one of the procedures for distinguishing the relative quality of bay-estuarine habitats and deserves to be tested in additional localities. The results for Morro Bay also underscore the need for a more thorough knowledge of its fish communities since it is a relatively pristine habitat that may be subject to a number of alterations in the future (Gerdes et al. 1974).

[2]Millicent L. Quammen, graduate student, Department of Biological Science, University of California, Santa Barbara, CA 93106, pers. commun. August 1979.

ACKNOWLEDGMENTS

I especially thank S. Marie Harvey who contributed significantly to the completion of this study. She ably assisted in the field work, meticulously recorded and compiled the data, and carefully drafted the figures. I greatly appreciate the efforts of Larry Allen, Gregory Smith, and Wayne White who showed unwavering support of the project throughout its duration. They, along with James Knost, Linda Sims, Robert Sims, and John Tiedeman, performed tirelessly and enthusiastically during the long hours of field work. I am grateful to the numerous other people who assisted with the data collection, including David Chapman, Myra Chapman, Gary Devian, Richard Dumke, Wanda Halbakken, Kathryn Heath, Kheryn Klubnikin, Lee Lorenzen, Margaret Neighbors, Sarah Swank, Denise White, and Robert White. I extend sincere thanks to Millicent Quammen who kindly made available to me her unpublished data on Mugu Lagoon fishes. Financial assistance and material support were provided by the Department of Biology, California State University, Fullerton.

LITERATURE CITED

ALLEN, L. G.
1976. Abundance, diversity, seasonality and community structure of the fish populations of Newport Bay, California. M.A. Thesis, Calif. State Univ., Fullerton, 108 p.

ALLEN, L. G., AND M. H. HORN.
1975. Abundance, diversity and seasonality of fishes in Colorado Lagoon, Alamitos Bay, California. Estuarine Coastal Mar. Sci. 3:371-380.

BANE, G., AND M. ROBINSON.
1970. Studies on the shiner perch, *Cymatogaster aggregata* Gibbons, in upper Newport Bay, California. Wasmann J. Biol. 28:259-268.

BECHTEL, T. J., AND B. J. COPELAND.
1970. Fish species diversity indices as indicators of pollution in Galveston Bay, Texas. Contrib. Mar. Sci. 15:103-132.

FIERSTINE, H. L., K. F. KLINE, AND G. R. GARMAN.
1973. Fishes collected in Morro Bay, California between January, 1968, and December, 1970. Calif. Fish Game 59:73-88.

FREY, H. W. (editor).
1971. California's living marine resources and their utilization. Resour. Agency, Calif. Dep. Fish Game, 148 p.

FREY, H. W., R. F. KLEIN, AND J. L. SPRUILL.
1970. The natural resources of Upper Newport Bay and recommendations concerning the bay's development. Resour. Agency, Calif. Dep. Fish Game, 68 p.

FRONK, R. H.
1969. Biology of *Atherinops affinis littoralis* Hubbs in Newport Bay. M.S. Thesis, Univ. California, Irvine, 106 p.

GERDES, G. L., E. R. J. PRIMBS, AND B. M. BROWNING.
1974. Natural resources of Morro Bay, their status and future. Calif. Dep. Fish Game Coastal Wetlands Ser. 8:1-103.

HAEDRICH, R. L.
1975. Diversity and overlap as measures of environmental quality. Water Res. 9:945-952.

HOESE, H. D., B. J. COPELAND, F. N. MOSELEY, AND E. D. LANE.
1968. Fauna of the Aransas Pass Inlet, Texas. III. Diel and seasonal variations in trawlable organisms of the adjacent area. Tex. J. Sci. 20:33-60.

HOFF, J. G., AND R. M. IBARA.
1977. Factors affecting the seasonal abundance, composition and diversity of fishes in a southeastern New England estuary. Estuarine Coastal Mar. Sci. 5:665-678.

HORN, M. H., AND L. G. ALLEN.
In press. Ecology of fishes in upper Newport Bay, California: seasonal dynamics and community structure. Calif. Dep. Fish Game, Mar. Resour. Tech. Rep.

JONES, A. C.
1962. The biology of the euryhaline fish *Leptocottus armatus armatus* Girard (Cottidae). Univ. Calif. Publ. Zoöl. 67:321-367.

LIVINGSTON, R. J.
1976. Diurnal and seasonal fluctuations of organisms in a north Florida estuary. Estuarine Coastal Mar. Sci. 4:373-400.

MACDONALD, K. B.
1976. The natural resources of Mugu Lagoon. Calif. Dep. Fish Game, Coastal Wetland Ser. 17:1-119.

MCCLEAVE, J. D., AND S. M. FRIED.
1975. Nighttime catches of fishes in a tidal cove in Montsweag Bay near Wiscasset, Maine. Trans. Am. Fish. Soc. 104:30-34.

ODENWELLER, D. B.
1975. The life history of the shiner surfperch *Cymatogaster aggregata* Gibbons, in Anaheim Bay, California. *In* E. D. Lane and C. W. Hill (editors), The marine resources of Anaheim Bay, p. 107-115. Calif. Dep. Fish Game, Fish Bull. 165.

SUBRAHMANYAM, C. B., AND S. H. DRAKE.
1975. Studies on the animal communities in two north Florida salt marshes. Part I. Fish communities. Bull. Mar. Sci. 25:445-465.

TASTO, R. N.
1975. Aspects of the biology of Pacific staghorn sculpin, *Leptocottus armatus* Girard, in Anaheim Bay. *In* E. D. Lane and C. W. Hill (editors), The marine resources of Anaheim Bay, p. 123-135. Calif. Dep. Fish Game, Fish Bull. 165.

WALLACE, J. H.
1975. The estuarine fishes of the East coast of South Africa. I. Species composition and length distribution in the estuarine and marine environments. II. Seasonal abundance and migrations. S. Afr. Assoc. Mar. Biol. Res., Oceanogr. Res. Inst. Invest. Rep. 40, 72 p.

WHITTAKER, R. H., AND C. W. FAIRBANKS.
1958. A study of plankton copepod communities in the Columbia Basin, southeastern Washington. Ecology 39:46-65.

MOVEMENTS OF TAGGED AMERICAN LOBSTER, *HOMARUS AMERICANUS*, OFF RHODE ISLAND[1]

MICHAEL J. FOGARTY,[2] DAVID V. D. BORDEN,[3] AND HOWARD J. RUSSELL[4]

ABSTRACT

In 1974 and 1975 a total of 3,063 American lobster, *Homarus americanus*, were tagged and released at five sites along the Rhode Island coast and on the adjacent continental shelf. Analyses were based on 671 returns with sufficient information to assess movement patterns. Lobster movements at inshore locations were generally localized; the mean distance between release and recovery sites ranged from 5.5 to 10.4 km. Intense fishing effort in inshore areas resulted in a disproportionate number of returns within 30 days of release. Rayleigh tests demonstrated a nonuniform ($P<0.01$) distribution of return directions at each site. Mean vector angles ranged from 164.5° to 193.7° from true north at inshore locations.

Lobsters tagged and released on Cox Ledge, 35 km southeast of Narragansett Bay, migrated to the outer continental shelf in late fall and winter. The mean distance travelled was 41.6 km and the average time between release and recapture was 235.3 days. A Rayleigh test indicated that the distribution of return directions was nonuniform ($P<0.01$) and the mean vector angle was 158.8° from true north.

Analyses of the movement patterns of the American lobster, *Homarus americanus*, in coastal waters have typically revealed little evidence of extensive migrations. In a study designed to examine seasonal movements, Wilder and Murray (1958) noted a mean dispersion radius of <1.6 km for tagged lobsters released off the coast of Nova Scotia. Wilder (1963) reported movements averaging 13.5 km for tagged lobsters at large 10-12 mo off Price Edward Island. Bergeron (1967) concluded that lobsters undertake a seasonal onshore-offshore migration of about 10 km off the Magdalen Islands of Quebec. In tagging experiments conducted in the Gulf of Maine, Cooper (1970) and Krouse[5] noted generally localized movements. Dow (1974) indicated, however, that large lobsters (>127 mm carapace length, CL) may undertake migrations of over 140 km. Morrissey (1971) presented evidence for directed movements averaging 26.1 km for ovigerous and sublegal-sized lobsters in the southern Gulf of Maine. Lund et al.[6] reported that lobsters tagged in western Long Island Sound were nonmigratory while others tagged in eastern Long Island Sound undertook migrations to the edge of the continental shelf.

In contrast, Cooper and Uzmann (1971) and Uzmann et al. (1977) demonstrated an extensive inshore spring migration for lobsters tagged on the outer continental shelf. Saila and Flowers (1968) reported that ovigerous females displaced from continental shelf waters to Narragansett Bay, R.I., tended to return to the area of first capture.

The present study was designed to examine various aspects of the population dynamics of lobster off the coast of Rhode Island. In this paper we describe the movement and migratory behavior of lobster in local waters. The work was part of a coast-wide research effort sponsored by the State-Federal Lobster Management Program under the auspices of the U.S. Department of Commerce, National Marine Fisheries Service, with the objective of developing a comprehensive management strategy for lobster in the territorial waters of the United States.

[1]This study was conducted in cooperation with the U.S. Department of Commerce, National Marine Fisheries Service, under grant 03-4-043-360.

[2]Division of Fish and Wildlife, Rhode Island Department of Environmental Management, Wickford, R.I.; present address: Northeast Fisheries Center Woods Hole Laboratory, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543.

[3]Division of Fish and Wildlife, Rhode Island Department of Environmental Management, 150 Fowler St., Wickford, RI 02852.

[4]Division of Fish and Wildlife, Rhode Island Department of Environmental Management, Wickford, R.I.; present address: New England Regional Fisheries Management Council, Peabody, MA 01960.

[5]Krouse, J. S. 1977. Lobster tagging project No. 3-228-R. Project completion report. Maine Department of Marine Resources, West Boothbay Harbor, Maine, 29 p.

[6]Lund, W. A., L. L. Stewart, and C. J. Rathbun. 1973. Investigation on the lobster. Completion report. Commercial Fisheries Research and Development Act. Project 3-130-R, 189 p. Univ. Connecticut, Storrs, Conn.

Manuscript accepted February 1980.
FISHERY BULLETIN: VOL. 78, NO. 3, 1980.

METHODS

In 1974 and 1975, 3,063 lobsters (55-176 mm CL) were tagged and released at five general locations off the Rhode Island coast and on the adjacent continental shelf (Figure 1).

Lobsters were tagged using the sphyrion anchor tag (Scarratt and Elson 1965). The tag consisted of an encoded yellow plastic tube (2 mm in diameter) attached to a stainless steel anchor by a monofilament thread. The anchor was inserted with a hypodermic needle into the right or left dorsal extensor muscle of the lobster through the membrane posterior to the margin of the carapace. Carapace length, sex, molt status, and physical condition were recorded for each tagged lobster. We obtained lobsters used in tagging experiments directly aboard commercial lobster vessels. Lobsters were tagged at sea and released as close to the point of capture as possible. However, on 20 December 1974, 231 lobsters captured on the mid-continental shelf (Midshelf) were released on Cox Ledge. This displacement (≈60 km) was necessary to avoid several foreign trawlers which moved into the area during tagging operations.

Rewards of $2 for the return of the tag alone and $5 for the return of the lobster and tag were paid. Information on the date and location of capture were requested for each recapture. The study was publicized through the local news media, posters describing the study distributed to shellfish dealers, and personal contact with fishermen.

For detailed evaluation of directional components of movement we followed the approach of Saila and Flowers (1968). The specific test statistics and directional components computed were

Mean vector angle $\bar{\Theta} = \arctan\left[\frac{\sum r \sin \Theta}{\sum r \cos \Theta}\right]$

Mean square dispersion coefficient (km^2/d)

$$a^2 = \frac{1}{n}\left[\sum \frac{r^2}{t} - \frac{(\sum r \cos \Theta)^2 + (\sum r \sin \Theta)^2}{\sum t}\right]$$

North-south directional component (km/d) $V = \frac{\sum r \cos \Theta}{\sum t}$

East-west directional component (km/d) $V' = \frac{\sum r \sin \Theta}{\sum t}$

Rayleigh test statistic $Z = R^2/n$

where $R = [(\sum \sin \Theta)^2 + (\sum \cos \Theta)^2]^{1/2}$

n = number of individuals

Θ = direction of travel from an arbitrary reference point

t = time in days from release

r = straight line distance (km) of travel.

All angles are presented as deviations from true north (°T). The Rayleigh test is a test for uniform concentration of points around a circle of unit radius (Batschalet 1965).

The mean square dispersion coefficient is a measure of undirected or random movement based on diffusion theory (Beverton and Holt 1957; Jones 1959, 1966). The dispersion coefficient is a compound parameter dependent on both rate of travel and the mean distance travelled without directional change (Jones 1959). The quantities V and V' indicate directional or nonrandom components of movement. These parameters measure the mean rate of group movement of tagged individuals in the north-south and east-west planes.

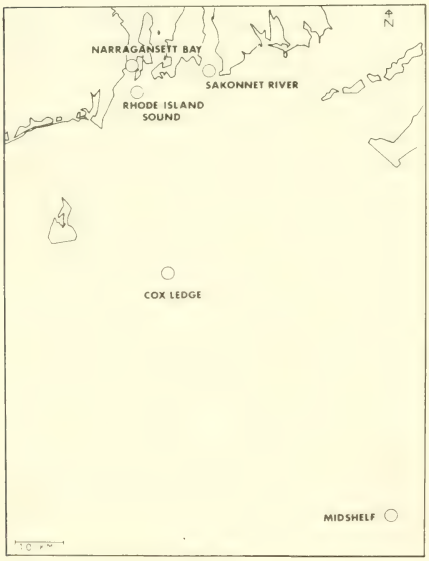


FIGURE 1.—Location of tagging sites for American lobster in the coastal waters of Rhode Island and on the adjacent continental shelf.

RESULTS

Inshore Locations

To date, 450 lobsters tagged and released at coastal sites have been recovered with sufficient information to assess movement patterns (Table 1). Due to intensive fishing effort for lobster along the Rhode Island coast, a disproportionate number of tags were returned within 30 d of release (Figure 2); the mean time at large was 48.6, 34.7, and 48.6 d for lobsters released in Narragansett Bay, Rhode Island Sound, and the Sakonnet River. Most lobsters tagged at inshore locations were recaptured within 6 km of the release site (Figure 3), possibly reflecting the short time at large. The distance between release and recovery sites averaged 6.9, 10.4, and 5.5 km at the Narragansett Bay, Rhode Island Sound, and Sakonnet River locations. Distance travelled tended to increase with time up to 90 d at large at each inshore location although high variability made clear trends difficult to discern (Figure 4).

An initial examination of straight-line tracks between release and recapture sites revealed a general southerly trend in movements for lobsters released at inshore tagging sites (Figure 5). These plots also demonstrated that some inshore lobsters

TABLE 1.—Release and recapture data for American lobsters tagged in 1974 and 1975 off Rhode Island. Locales are given in Figure 1. Number recaptured refers to the number of returns with adequate information to evaluate movements. Cox Ledge-Midshelf indicates lobsters captured on the midcontinental shelf (Midshelf) and released on Cox Ledge.

Release site	Release period	Number released	Recaptured		Carapace length (mm) at release		
			No.	%	Mean	SE	Range
Sakonnet River	15 May-31 July 1975	645	147	22.79	80.57	0.257	62.0-103.0
Rhode Island Sound	9 May-21 Aug. 1975	543	115	21.18	79.02	.286	55.0-108.0
Narragansett Bay	9 May-15 Nov. 1975	470	188	40.00	73.92	.212	58.0-102.0
Cox Ledge	11 Nov.-5 Dec. 1974	612	157	25.65	82.70	.454	62.0-134.0
Cox Ledge-Midshelf	20 Dec. 1974	231	29	12.55	96.67	1.201	64.0-167.0
Midshelf	29 Oct.-18 Nov. 1974	562	34	6.05	86.92	.637	65.0-176.0

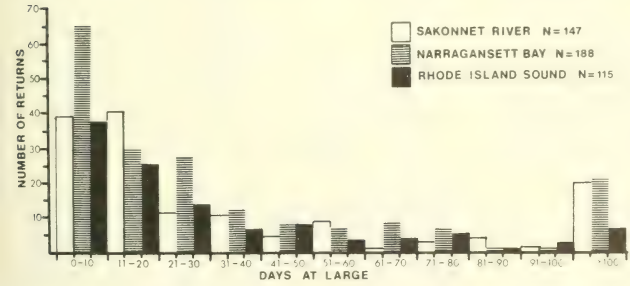


FIGURE 2.—Number of tag returns for American lobster released at inshore locations off Rhode Island as a function of time at large.

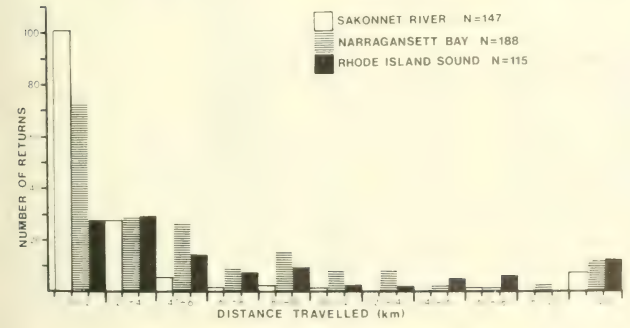
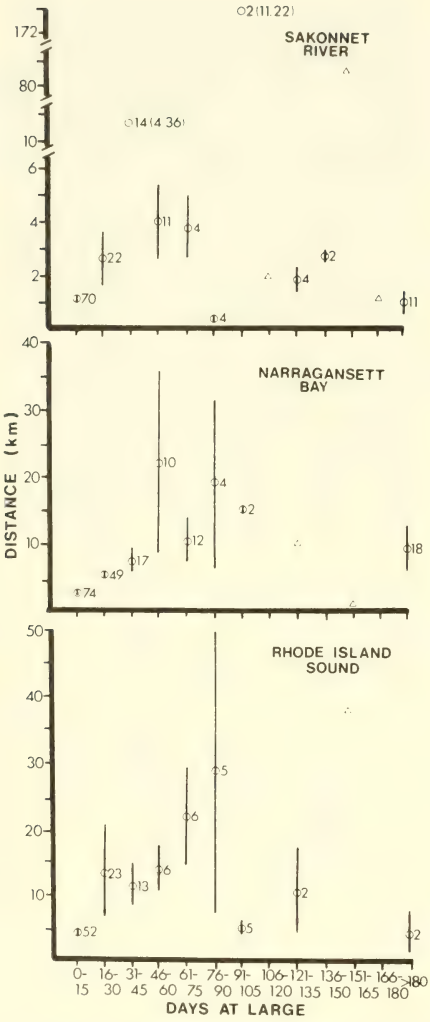
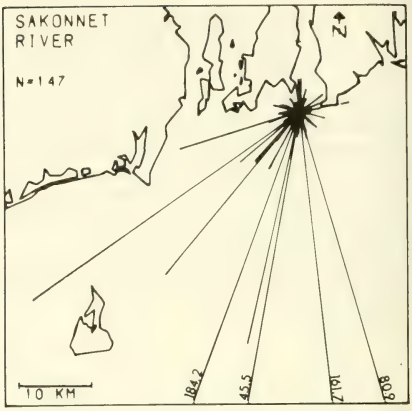
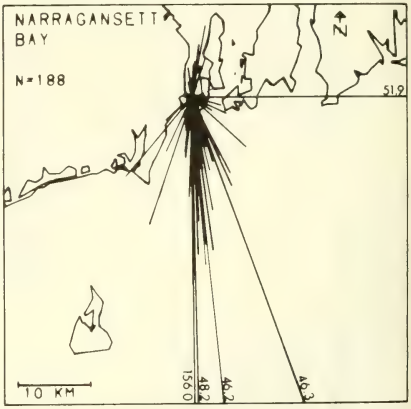


FIGURE 3.—Number of tag returns for American lobster released at inshore locations off Rhode Island as a function of distance travelled.







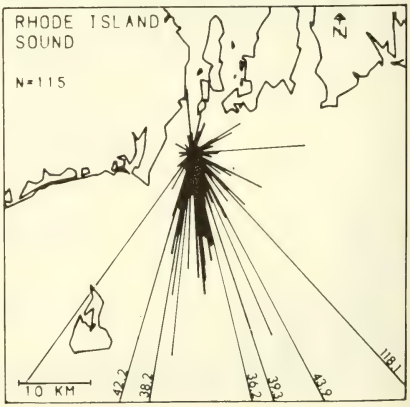


FIGURE 4.—Distance travelled ($\bar{x} \pm 1$ SE) as a function of time at large for tagged American lobster released at inshore locations off Rhode Island. Open triangles denote single observations for the time period. Sample sizes are specified beside each mean with an associated standard error. Standard errors are provided in parentheses for observations falling within ranges of truncated ordinate.

FIGURE 5.—Straight line distance between release and recovery sites for American lobster at inshore locations off Rhode Island. Release locations are composites of several release sites in each area. Total distance travelled is noted for tracks which are truncated by borders.

did undertake extensive movements. Appropriate test statistics and directional components (Saila and Flowers 1968) were computed for each total data set and for data partitioned according to time at large (Table 2). Missing data for some returns prevented the use of all the recoveries for these analyses. Mean vector angles ($\bar{\Theta}$) for the three locations ranged from 164.53°(T) to 193.69°(T), and Rayleigh tests indicated a nonuniform distribution of returns at each inshore location (Table 2). In general, the north-south vector components were consistently stronger than the east-west components for each location. When partitioned by time at large, the relative magnitude of the north-south and east-west vector components were more nearly equal for the first time period (0-20 d) at the Sakonnet River site, possibly reflecting an initial random dispersal of released lobsters. The lack of a statistically significant mean vector bearing for this period (Table 2) supports this inference.

The consistently low estimates of V' for lobsters tagged at inshore locations were due, in part, to physiographic constraints since east-west movements were often limited by the coastline, particularly in Narragansett Bay (Figure 1). The negative north-south vector components were indicative of net southerly movement since the cosine of angles ranging from 90° to 270° would be negative. Similarly, negative values of V' imply a westerly displacement since the sine of angles from 180° to 360° would be negative.

The mean square dispersion coefficient (a^2) varied considerably by location and the time period under consideration (Table 2). The quantity a^2 measures the relative degree of undirected movement of any individual with respect to the group directional average. Some caution is necessary in interpreting these values since dispersion coefficients are likely to be overestimated when movements are nonrandom (Jones 1959).

To examine the possibility of directed seasonal movements, we pooled data from inshore release locations and regrouped them according to release period and time at large. We compared movement statistics for lobsters released prior to 1 July 1975 and recaptured prior to 1 September 1975 with those released after 1 July 1975 and recaptured prior to 1 September 1975 (Table 3). We noted a nonuniform distribution of returns at all levels of analysis (Table 3). The north-south directional components consistently dominated the east-west components for both groups. The negative V values reflect the strong southerly directionality for both groups while the east-west components (V') varied considerably when further partitioned by time at large (Table 3). For lobsters released after 1 July 1975 the north-south vector components were two to three times higher than for late spring-early summer releases, indicating a sharp in-

TABLE 2.—Mean vector angle ($\bar{\Theta}$) from true north, mean square dispersion coefficient (a^2), north-south (V) and east-west (V') directional components, Rayleigh test statistics (R and Z) and sample size (n) for lobsters released in the Sakonnet River, Narragansett Bay, Rhode Island Sound, and Cox Ledge. The mean square dispersion coefficient is a measure of random movements; V and V' indicate nonrandom components of movement. Negative values of V and V' are indicative of net southerly and westerly movements. The Rayleigh test is a test for uniform concentration of points around a circle of unit radius.

Location	Days at large	$\bar{\Theta}$ (°T)	a^2 (km²/d)	V (km/d)	V' (km/d)	R	Z	n
Sakonnet River	0-20	215.236	1.952	−0.077	−0.054	10.225	2.133	49
	21-60	211.748	4.966	− .119	− .074	11.391	4.805**	27
	>61	184.469	25.574	− .104	− .008	6.418	1.647	25
	Total	193.694	8.654	− .105	− .025	26.899	7.164**	101
Narragansett Bay	0-20	175.072	2.870	− .294	.025	34.238	13.630**	86
	21-60	178.854	11.012	− .293	.006	31.339	20.043**	49
	>61	164.301	2.471	− .054	.015	24.982	17.336**	36
	Total	173.353	5.700	− .123	.014	90.178	47.556**	171
Rhode Island Sound	0-20	167.967	8.597	− .340	.073	26.958	11.913**	61
	21-60	163.498	2.872	.246	.073	23.207	17.951**	30
	>61	163.212	9.840	− .140	.042	12.650	7.620**	21
	Total	164.530	7.502	− .199	.055	62.241	34.589**	112
Cox Ledge	0-180	162.690	38.155	−1.244	.388	22.559	14.968**	34
	181-270	140.637	16.365	− .062	.051	8.077	1.553	42
	271-360	150.263	6.900	− .048	.027	15.856	4.261	59
	>361	150.549	14.166	− .104	.059	3.222	1.483	7
	Total	154.847	4.931	− .120	.056	37.863	10.096	142

**$P<0.01$.

TABLE 3.—Movement statistics for lobsters released prior to 1 July 1975 and recaptured prior to 1 September 1975 (spring-early summer) and lobsters released after 1 July 1975 and recaptured prior to 1 September 1975 (late summer). Data are pooled over release locations in Narragansett Bay, Rhode Island Sound, and the Sakonnet River. See Table 2 for explanation of symbols.

Season	Days at large	θ (°T)	a^2 (km²/d)	V (km/d)	V (km/d)	R	Z	n
Spring-early summer	0-15	190.657	3.038	−0.156	−0.029	22.287	5.458**	91
	16-30	165.275	1.368	− .104	.027	16.365	5.251**	51
	31-45	183.151	2.247	− .144	− .008	16.946	9.573	30
	46-60	180.343	22.126	− .249	− .001	13.945	9.260**	21
	>61	183.380	12.854	− .110	.006	22.201	14.935**	33
	Total	178.854	5.852	− .138	.003	91.056	36.687**	226
Late summer	0-15	161.321	7.121	− .473	.160	33.975	18.035**	64
	16-30	188.365	4.527	− .479	− .070	15.036	10.765**	21
	>30	202.517	8.495	− .434	− .180	4.531	4.105**	5
	Total	179.427	6.808	− .469	− .005	52.447	30.563**	90

**$P<0.01$

crease in directional movement in this period. Estimates of the mean square dispersion coefficient also increased in the late summer period, indicating a general increase in activity levels. The relative magnitude of the increase in random movement (as measured by a^2) was less striking than the increase in directed movement, however (Table 3).

A two-way fixed factor analysis of variance was used to determine the effects of size and sex on distance travelled for each inshore release location. The three inshore sites differed slightly in release periods (Table 1) and were therefore treated independently to eliminate any possible seasonal effects. Lobsters were categorized on the basis of release size (≤60, 61-70, 71-80, 81-90, >91 mm CL) and sex (male, female, ovigerous female). No significant differences ($P<0.01$) were noted by size, sex, or the size-sex interaction at any of the three release locations. The data were treated with a $\log_e(x+1)$ transform prior to analysis.

Offshore Locations

In contrast to lobsters tagged at coastal locations, those tagged and released on Cox Ledge exhibited extensive movements. The mean distance travelled was 41.6 km and the average time between release and recapture was 235.3 d. Return rates were relatively high for the first 30 d, and subsequently increased for lobsters at large over 240 d (Figure 6). Of 157 lobsters recovered with adequate information to evaluate movements, 117 (74.5%) were recaptured within 60 km of the release site (Figure 7). Examination of dispersal as a function of time at large indicated large-scale movements within 60-120 d of liberation while recoveries after 240 d were progressively closer to the release site (Figure 8). Plots of

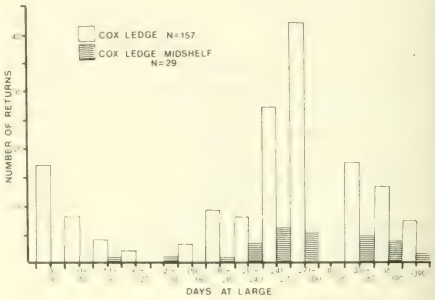


FIGURE 6.—Number of tag returns for American lobster released on Cox Ledge and lobster displaced from the Midshelf tagging site to Cox Ledge (Cox Ledge-Midshelf) as a function of time at large, Rhode Island vicinity.

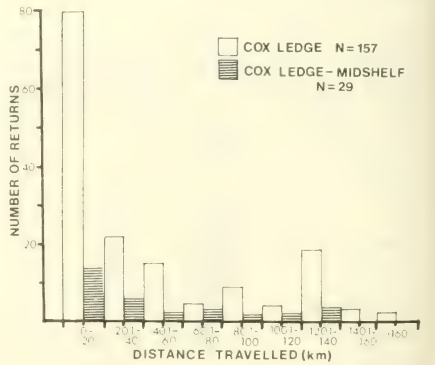


FIGURE 7.—Number of tag returns for American lobster released on Cox Ledge and lobster displaced from the Midshelf tagging site to Cox Ledge (Cox Ledge-Midshelf) as a function of distance travelled, Rhode Island vicinity.

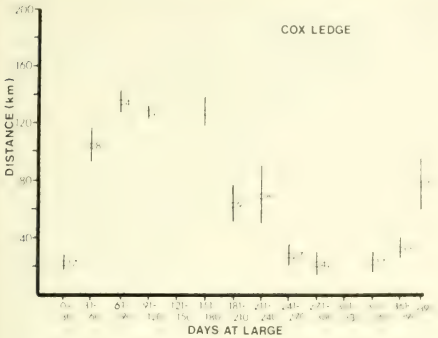


FIGURE 8.—Distance travelled ($\bar{x} \pm 1$ SE) as a function of time at large for American lobster tagged and released on Cox Ledge, off Rhode Island. Sample sizes are specified beside each mean with an associated standard error.

straight-line distance between release and recovery sites indicated that these long distance migrants travelled to the outer continental shelf (Figure 9).

Tagging experiments conducted on the outer continental shelf revealed a shoalward migration in late spring and summer (Cooper and Uzmann 1971; Uzmann et al. 1977). The offshore migration in late fall and winter observed in the present study complements these findings and indicates a seasonal interchange between areas.

The mean vector angle for recovered tagged lobsters was 154.8°(T) at the Cox Ledge site and Rayleigh tests indicated a nonuniform distribution of returns (Table 2). The north-south vector component was substantially higher than the east-west component for the first 180 d at large, reflecting the strongly directed offshore movement. The relative magnitude of the north-south and east-west vector components were more nearly equal for lobsters at large over 180 d, indicating little directed movement. This is reflected in the nonsignificant mean vector bearing for lobsters at large between 181 and 270 d (Table 2).

A two-way fixed factor analysis of variance was used to examine the effects of size and sex on distance travelled for lobsters tagged and released on Cox Ledge. Lobsters were grouped by release size (≤90, 91-100, 101-110, 111-120, 121-130, ≥131 mm CL) and sex (male, female, ovigerous female) and the data were transformed ($\log_e x+1$) prior to analysis. No significant differences ($P<0.01$) were noted by size, sex, or the size-sex interaction.

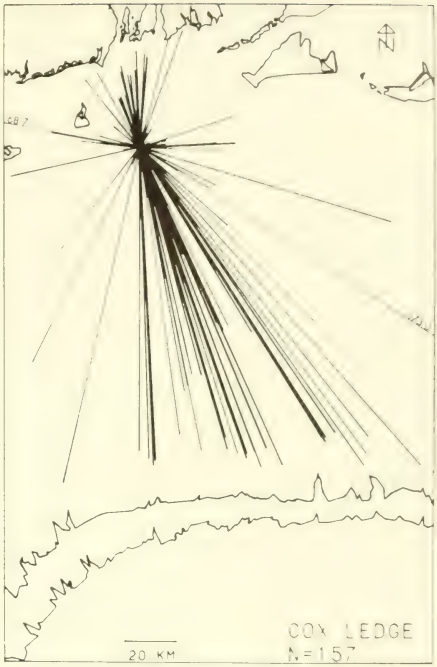


FIGURE 9.—Straight line distance between release and recapture sites for American lobster tagged and released on Cox Ledge, off Rhode Island. Release location is a composite of four release sites on Cox Ledge. Total distance travelled is noted for tracks which are truncated by borders.

Low return rates ($n=29$) for lobsters displaced from the Midshelf site to Cox Ledge prevented detailed analysis of movement patterns. The displaced lobsters were treated independently of the lobsters tagged and released on Cox Ledge at all levels of analysis. The mean distance travelled for lobsters transplanted from the Midshelf site to Cox Ledge was 41.6 km with an average of 274.7 d between release and recapture. The mean vector bearing for Cox Ledge-Midshelf lobsters was 170.5°(T); however, the hypothesis of a uniform distribution of return directions was not rejected ($P<0.01$) when the data were subjected to a Rayleigh test.

Return rates for lobsters tagged and released on the Midshelf fishing grounds were also low, preventing detailed analysis. The mean distance travelled for 34 recovered lobsters was 18.2 km and

the mean time at large was 26.9 d. The mean vector angle for Midshelf lobsters was 167.1°(T) and the distribution of return directions was nonuniform (Rayleigh test; $P<0.01$).

DISCUSSION

Tagging experiments conducted in the coastal waters of the western North Atlantic have demonstrated generally localized lobster movements. Recent in situ observations in restricted regions of the Gulf of Maine (Cooper et al. 1975) and in Long Island Sound (Stewart 1972) have supported these results using seasonal underwater census techniques. Morrissey (1971) and Dow (1975) demonstrated, however, that lobsters tagged at inshore locations were capable of undertaking large-scale movements. Lund et al. (footnote 6) reported that some lobsters tagged in eastern Long Island Sound migrated to the outer continental shelf. Direct comparisons among these inshore studies are often not possible due to differences in tagging methodology, seasonal deployment of tags, and size range of lobsters tagged.

More consistent long-range movement patterns have been noted for lobsters tagged and released on the outer continental shelf (Cooper and Uzmann 1971; Uzmann et al. 1977). Saila and Flowers (1968) had earlier demonstrated that ovigerous female lobsters were capable of extensive movements when displaced from offshore sites to Narragansett Bay.

In the present study, the movements of lobsters tagged and released at inshore locations were typically localized. We attributed the small dispersion radius, in part, to high exploitation rates which resulted in rapid recovery of released lobsters. Examination of recapture records indicated that some inshore lobsters at large for over 180 d exhibited little movement. Unfortunately, it is impossible to determine the actual trajectories of recovered lobsters and the true extent of movements between release and recovery is unknown. Employing an ultrasonic tag, Lund et al. (footnote 6) tracked individual lobster movements and concluded that most lobsters undertake only minor (<30 m) daily movements in eastern Long Island Sound.

We consistently noted southerly movements for recaptured lobsters released at inshore locations. Constraints on east-west and northerly movements imposed by geographical features of the area undoubtedly contributed to this result although movement was not totally precluded in these directions (Figure 1). The Rayleigh test gives equal weight to each return direction and therefore any detectable movement in any direction would be represented in the analysis.

Nonuniform distribution of fishing effort further complicates the interpretation of these results and the potential bias introduced by this factor cannot be ignored. Nonhomogeneous sampling effort can result in an apparent directional tendency when superimposed on random movements. In the lobster fishery, effort is concentrated primarily in areas with available shelter where lobster density is highest. Lund et al. (footnote 6) reported that lobster movements at inshore locations were often transitions between areas of suitable habitat. Dispersal of this type is therefore likely to be detected through returns from the commercial fishery. Due to high demand for lobster, the coverage exerted by the fishery is extensive and it has expanded to areas which were formerly considered marginal in terms of catch per unit effort or where operational costs were prohibitive (as on the outer continental shelf). The distribution of effort therefore generally approximates the distribution of lobster.

Comparisons between lobsters released at inshore locations in spring and early summer with those released in late summer indicated a sharp increase in directed movements in the latter period. A concommitant increase in the mean square dispersion coefficient indicated that random movements also increased, possibly as a result of increased activity and catchability. The timing of release differed slightly at each of the inshore locations; of the 147 lobsters recovered from the Sakonnet River tagging, 119 (80.9%) had been released prior to 1 July while 123 (65.4%) and 59 (51.3%) of the Narragansett Bay and Rhode Island Sound lobsters were released prior to 1 July. Since the three inshore release sites were located in close proximity and were similar habitat types, we attributed the differences in movements between locations to the timing of release. Stewart (1972) noted increased activity and movements in summer for lobsters tagged in Long Island Sound.

In constrast to the limited movements noted at inshore release locations, lobsters tagged on Cox Ledge migrated to the outer continental shelf in late fall and winter. Little evidence of lateral movement was noted despite an active fishery to both the east and west of Cox Ledge. Coupled with observations of an inshore spring migration from

the outer continental shelf (Cooper and Uzmann 1971; Uzmann et al. 1977), these data indicate an intermixing between offshore and inshore lobster populations. Independent confirmation of seasonal inshore-offshore movements has been obtained using a stratified random trawl survey conducted in spring and fall by the National Marine Fisheries Service (Burns et al.[7]).

Lobster stock identification studies based on electrophoretic techniques (Tracey et al. 1975) and linear discriminant analysis of morphometric data (Saila and Flowers 1969) indicated that inshore and offshore groups are discrete. Tracey et al. (1975) noted generally low levels of genetic variability, but inshore and offshore lobsters were differentiable at one locus of the 44 examined. Saila and Flowers (1969) reported significant profile differences between inshore and offshore lobsters. These studies would indicate that inshore and offshore groups retain their genetic identity despite seasonal intermixing. Migrational studies do indicate the possibility of genetic exchange between areas, perhaps explaining the low levels of genetic variability (Tracey et al. 1975) and some of the inconsistencies noted by Saila and Flowers (1969). The period of intermixing does correspond to periods of molting and mating activity. Further research on inshore-offshore stock interactions is clearly needed to resolve these questions. This factor assumes particular importance since it is possible that coastal sites are dependent on recruitment from offshore areas to sustain inshore populations that are subjected to extremely high levels of fishing mortality.

ACKNOWLEDGMENTS

We would like to express our appreciation to Richard Sisson, Timothy Lynch, Arthur Ganz, and James Herrmann for assistance in the field. James Yoder kindly provided a computer program for analysis of movements. We are grateful to Barbara Simon and Ellen Yoder for programming and data management and to Linda Gray for typing the manuscript. Thomas D. Morrissey, Saul B. Saila, and J. Stanley Cobb critically read the manuscript and offered many helpful suggestions.

[7]Burns, T. S., S. H. Clark, V. C. Anthony, and R. J. Essig. 1979. Review and assessment of the USA offshore lobster fishery. Int. Cons. Explor. Mer Shellfish Comm. C.M. 1979/K:25, 31 p.

LITERATURE CITED

BATSCHALET, E.
1965. Statistical methods for the analysis of problems in animal orientation and certain biological rhythms. Am. Inst. Biol. Sci., 57 p.

BERGERON, J.
1967. Contribution à la biologie du homard (*Homarus americanus* M. Edw.) des Iles-de-la Madeleine. [Engl. Abstr.] Nat. Can. (Que.) 94:169-207.

BEVERTON, R. J. H., AND S. J. HOLT.
1957. On the dynamics of exploited fish populations. Minist. Agric. Fish. Food (G.B.) Fish. Invest., Ser. II, 19, 533 p.

COOPER, R. A.
1970. Retention of marks, their effects on growth, behavior, and migrations of the American lobster, *Homarus americanus*. Trans. Am. Fish Soc. 99:409-417.

COOPER, R. A., R. A. CLIFFORD, AND C. D. NEWELL.
1975. Seasonal abundance of the American lobster, *Homarus americanus*, in the Boothbay Region of Maine. Trans. Am. Fish. Soc. 104:669-674.

COOPER, R. A., AND J. R. UZMANN.
1971. Migrations and growth of deep-sea lobsters, *Homarus americanus*. Science (Wash., D.C.) 171:288-290.

DOW, R. L.
1974. American lobsters tagged by Maine commercial fishermen, 1957-59. Fish. Bull., U.S. 72:622-623.

JONES, R.
1959. A method of analysis of some tagged haddock returns. J. Cons. 25:58-72.
1966. Manual of methods of fish stock assessment. Part IV - Marking. FAO Fish. Biol. Tech. pap. 51, Suppl. 1, unpaged.

MORRISSEY, T. D.
1971. Movements of tagged American lobsters, *Homarus americanus*, liberated off Cape Cod, Massachusetts. Trans. Am. Fish. Soc. 100:117-120.

SAILA, S. G., AND J. M. FLOWERS.
1968. Movements and behaviour of berried female lobsters displaced from offshore areas to Narragansett Bay, Rhode Island. J. Cons. 31:342-351.

SCARRATT, D. J., AND P. F. ELSON.
1965. Preliminary trials of a tag for salmon and lobsters. J. Fish. Res. Board Can. 22:421-423.

STEWART, L. L.
1972. The season movements, population dynamics and ecology of the lobster, *Homarus americanus*, off Ram Island, Connecticut. Ph.D. Thesis, Univ. Connecticut, Storrs, 112 p.

TRACEY, M. L., K. NELSON, D. HEDGECOCK, R. A. SHLESER, AND M. L. PRESSICK.
1975. Biochemical genetics of lobsters: genetic variation and the structure of American lobster (*Homarus americanus*) populations. J. Fish. Res. Board Can. 32:2091-2101.

UZMANN, J. R., R. A. COOPER, AND K. J. PECCI.
1977. Migration and dispersion of tagged American lobsters, *Homarus americanus*, on the southern New England continental shelf. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-705, 92 p.

WILDER, D. G.
1963. Movements, growth and survival of marked and

tagged lobsters liberated in Egmont Bay, Prince Edward Island. J. Fish. Res. Board Can. 20:305-318.

WILDER, D. G., AND R. C. MURRAY.

1958. Do lobsters move offshore and onshore in the fall and spring? [In Engl. and Fr.] Fish. Res. Board Can., Prog. Rep. Atl. Coast Stn. 69:12-15.

FACTORS CONTROLLING GROWTH AND SURVIVAL OF CULTURED SPOT PRAWN, *PANDALUS PLATYCEROS*, IN PUGET SOUND, WASHINGTON

JOHN E. RENSEL[1] AND EARL F. PRENTICE[2]

ABSTRACT

Environmental factors affecting growth and survival of juvenile and yearling spot prawns, *Pandalus platyceros*, were studied at two sites in Puget Sound, Washington. It was thought that higher water temperatures at the southern site would promote increased growth rates, but intense plankton blooms and rapid fluctuations of water temperature induced high mortalities. Moribund prawns recovered quickly when placed in epibenthic cages that received cooler, relatively plankton-free water.

Although the cooler central Puget Sound site was judged suitable for prawn culture, fluctuations in temperature and plankton abundance caused moderate mortalities here as well.

Since 1970, several commercial marine aquaculture projects utilizing floating net pens for the culture of Pacific salmon, *Oncorhynchus* spp., (Mahnken 1975) have been developed in the Pacific Northwest. Development of companion crops to be grown in net pens with the salmon would enable growers to diversify and increase the return on their investments. The spot prawn, *Pandalus platyceros* Brandt, (herein referred to as prawn) may be a potential companion crop for several reasons: 1) it is adaptable to the sides as well as the bottom of net pens; 2) it can reproduce in captivity (Rensel and Prentice 1977); 3) it grows more rapidly and reaches a larger size than other pandalids (Butler 1964); 4) it consumes a variety of foods including dead fish; 5) it is gregarious and is normally not cannibalistic; and 6) it can be cultured in the laboratory (Wickins 1972; Kelly et al. 1976; Prentice[3]).

The objective of the present study was to determine the effects of environmental factors on growth and survival of juvenile and adult prawns held separately but near to salmon rearing pens at two differing salmon aquaculture sites. It was hypothesized that higher water temperatures at the more southern site would produce increased growth rates.

METHODS

Two sites were utilized for the experiments, Clam Bay and Henderson Inlet, both in Puget Sound, Wash. (Figure 1). At the National Marine Fisheries Service (NMFS) laboratory at Clam Bay, floating net pens for salmon research were situated at the end of a pier. Depth under the pens ranged from 9 to 14 m, depending on the stage of the tide. Data collected over several years indicated that the site had good water exchange with tidal currents reaching 0.4 kn at maximum flood and 1.0 kn at maximum ebb. The growth rate of prawns cultured previously at the site (Rensel and Prentice 1978) approximated that found in a wild population (Butler 1964).

The Henderson Inlet site (Figure 1) was at the location of a commercial log rafting operation. In 1973, a pilot-scale salmon aquaculture project was initiated by the Weyerhaeuser Company and the Washington Sea Grant Office at the site, and hydrographic data were collected (Snyder et al.[4]). Because of the inlet's shallow depth (10 m mid-channel), configuration, and location, seawater exchange is more restricted and tidal currents less

[1]Squaxin Island Tribe, Route 1, Box 257, Shelton, WA 98584.
[2]Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112.

[3]Prentice, E. F. 1975. Spot prawn culture: status and potential. *In* C. W. Nygaard (editor), Proceedings of a seminar on shellfish farming in Puget Sound, Oct. 7, 1975, Poulsbo, Wash. Processed Rep., 11 p. Wash. State Univ. Coll. Agric., Coop. Ext. Serv., Pullman, WA 99163.

[4]Snyder, B. P., A. J. Didier, Jr., and E. O. Salo. 1974. The culture of salmon at Willapa Bay, Grays Harbor, and Henderson Inlet in southern Puget Sound. Final Report Jan. 1973 to Feb. 1974. Univ. Wash., Coll. Fish., Fish. Res. Inst., Seattle, WA 98195, 211 p.

Manuscript accepted December 1979.
FISHERY BULLETIN: VOL. 78, NO. 3, 1980.

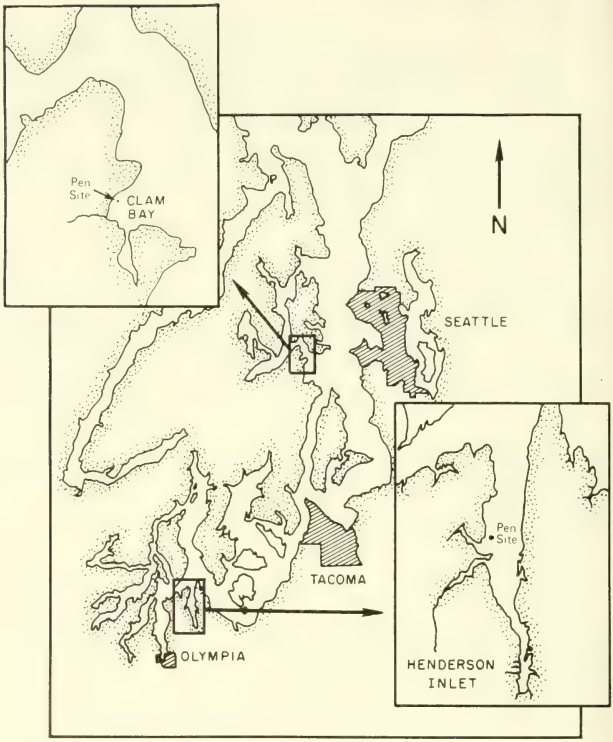


FIGURE 1.—Puget Sound, Washington, with sites of spot prawn studies at Henderson Inlet and Clam Bay.

than at Clam Bay. Surface water at the inlet was warmer and more turbid, but dissolved oxygen and salinity were similar to Clam Bay.

Five-month-old juvenile prawns, reared at the NMFS Clam Bay laboratory, were used in the study. The prawns were transferred to net pens and cultured from July to November 1974 at Henderson Inlet and from July 1974 until March 1975 at Clam Bay. Initial carapace lengths (distance from the base of the eyestalk to the posterior middorsal edge of carapace) of the juvenile prawns averaged 5.3 mm (n = 135 at each site, SD = 1.70) for all experimental lots. Weight of the prawns was not initially determined. We obtained wild prawns from commercial fishermen on Hood Canal (Puget Sound) in May 1974 and held them in a common pen for 3 wk at each site prior to distribution to rearing pens. The culture period was from June 1974 to March 1975. At the start of the experiment, the average carapace length was 25.8 mm (n = 336, SD = 1.68), and the average weight was 11.1 g (SD = 2.25). These prawns are referred to as yearlings as defined by the weight and length range (6.4-15.4 g, 21.2-28.5 mm) reported by Butler (1964) for a wild population.

Juvenile prawns were cultured in rectangular, knotless nylon net pens (stretched measure 6.7 mm), 2.16 m square × 1.8 m deep. Weights were attached externally to the corners of the pens to maintain their shape. Covers made of black plastic sheeting were placed over the pens to reduce light and discourage bird predation. Each pen was divided into three equal chambers by vertical net panels. The total immersed net area was 6.3 m^2/chamber. Each chamber was stocked with 45 prawns for an initial density of 7.1 prawns/m^2.

Pens used for the yearling prawns were also covered with plastic sheeting. These pens were the

same overall size and depth as the pens for the juveniles but were made of a larger mesh size (stretched measure, 9.0 mm) and not divided into chambers. Polyvinyl chloride pipe frames were placed in the pen bottoms to maintain the pen's shape. The total immersed substrate available to the prawns was 11.5 m^2/pen. Each pen was stocked with 112 prawns for an initial density of 9.7 prawns/m^2.

The prawns were divided into treatment groups based on age and diet. Juvenile prawns were fed raw meat of the blue bay mussel, *Mytilus edulis*. Yearling prawns were divided into two diet treatments. A "clam-fed" diet consisted of frozen processing waste from the geoduck, *Panope generosa*, which was fed without limit every other day after old food was removed. In a second treatment, "unsupplemented," the prawns were not fed but foraged on organisms growing on or drifting into the net pens. Dead prawns and exuviae were collected from each treatment every other day. All treatments were replicated three times at both test sites.

All surviving prawns were measured for length and weight except juveniles whose weights were estimated from carapace lengths using the formula $\log W = 2.93148 \log L = 3.07787$, where: L = length in millimeters and W = weight in grams (Butler 1964). Initially, the carapace of each juvenile prawn was measured to the nearest 0.1 mm with an ocular micrometer. Carapace length of yearlings was measured with calipers to the nearest 0.5 mm. Starting in October, the juvenile prawns were also measured with calipers. A top loading balance was used to obtain individual wet weights (nonblotted) of the prawns to the nearest 0.01 g.

RESULTS AND DISCUSSION

Environmental Data

Salinity at Henderson Inlet and Clam Bay ranged from 28.4 to 31.0‰, being within the range reported by Butler (1964) for wild prawn populations. Dissolved oxygen (DO) peaked in May (11.0 ppm at Henderson Inlet and 9.0 ppm at Clam Bay) and gradually fell to a minimum (5.0 ppm) in September at both sites. This low value at both sites only lasted a few hours during some tidal cycles. We believe these DO levels, because of their short duration and lack of stress on salmon in adjacent net pens, were adequate for the prawns and never caused stress. Bottom temperatures at Henderson Inlet were always higher than those at Clam Bay (Figure 2).

Light influences the growth of crustaceans. Forster (1970) reported significantly higher growth rates for juvenile prawns, *Palaemon serratus*, held in total darkness when compared with those held in other light conditions. A similar phenomenon has been reported with the American lobster, *Homarus americanus* (Conklen 1975). In our study, juvenile and yearling prawns avoided brightly illuminated areas and stopped feeding when the black covers were removed. This sudden increase in light intensity and the presence of an observer could have affected growth and survival, but no quantitative information was obtained.

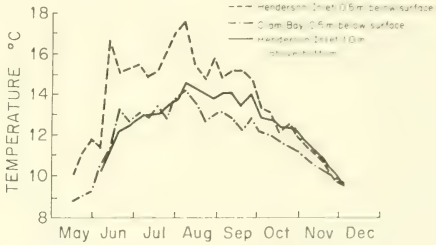


FIGURE 2.—Weekly mean water temperatures for Henderson Inlet and Clam Bay.

At Henderson Inlet, maximum water transparency, as measured with a Secchi disc, was from 0.5 to 4.2 m (5-d mean) less than at Clam Bay (Figure 3). Seasonal fluctuation in water transparency at both sites was caused by plankton blooms and runoff.

Growth and Survival of Juveniles

Between-site comparison of juvenile prawn growth was terminated in late November when Clam Bay juveniles were significantly heavier (t = 3.61, df = 2,147, $P<0.001$) (Figure 4) and longer (t = 3.35, df = 2,147, $P<0.002$) than those at Henderson Inlet. Growth monitoring continued at Clam Bay until March 1975.

Water temperature is an important factor affecting the growth of the spot prawn, and Wickins (1972) indicated that the optimum was at 18° C in the laboratory. During the period from July to September the maximum water temperatures at

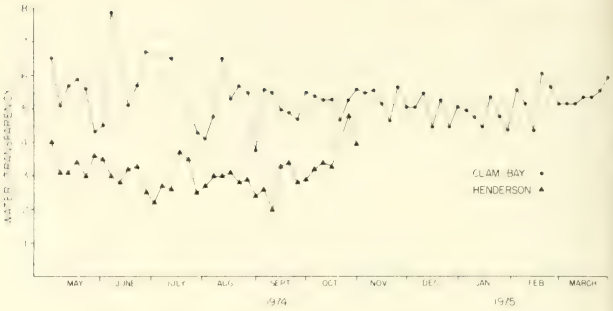


FIGURE 3.—Water transparency (5-d averages) at Henderson Inlet and Clam Bay as measured with a Secchi disc for the period May 1974 to March 1975.

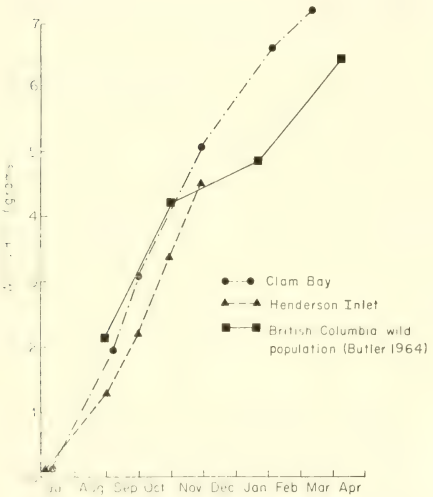


FIGURE 4.—Mean weights of juvenile spot prawns reared in net pens at Clam Bay and Henderson Inlet compared with a wild population in British Columbia (Butler 1964).

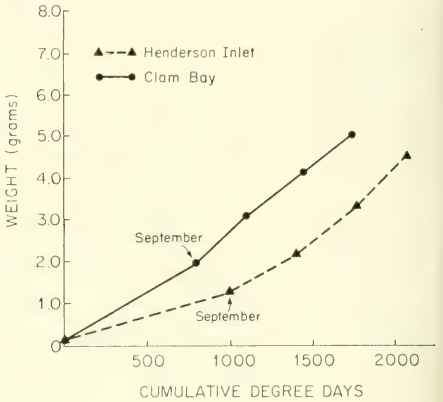


FIGURE 5.—Average weight of juvenile spot prawns as a function of cumulative degree days in the rearing experiments July to December 1974.

Henderson Inlet and Clam Bay were 19.0° and 16.5° C. Daily fluctuations up to 4° C were seen at both sites and the daily surface water temperatures at Henderson Inlet averaged 2.5° higher than at Clam Bay. The weekly mean temperatures never exceeded the optimal 18° C value at either site (Figure 2).

To evaluate the effect of temperature on the growth of juvenile prawns, the mean weight of the prawns was plotted against cumulative degree days (Figure 5). If temperature were the primary variable controlling growth within the prawns' zone of anabolism, then the curves (Figure 5) would be similar; however, this is not the case, as growth was depressed at Henderson Inlet. The slopes of both curves parallel each other after September, indicating that temperature had become the major factor affecting growth. Beginning in September there was a general decrease in water temperature at both sites (Figure 2).

To evaluate the growth of our prawns relative to the growth of wild populations, we compared our data with those of Butler (1964) who studied growth of a wild population in British Columbia. The data indicate the growth rate (increase in weight over time) of the cultured prawns was similar to that of the wild population up to the end of October (Figure 4). After October, the cultured

prawns continued to increase in weight at a relatively constant rate until the termination of the study. The wild population showed a decrease in growth rate during the period of late October to the end of January which was followed by a growth rate which approximated that of the cultured group. Water temperature and decreased availability of food are among the many factors which could account for the decreased growth in the wild populations.

At termination of comparative testing in November, total mortality of juvenile prawns was significantly greater ($\chi^2 = 67.2$, df = 1, $P<0.05$) at Henderson Inlet than at Clam Bay (Figure 6). The experiment at Clam Bay was continued to 10 March 1975, when survival was 79%.

We partially attribute the high mortality rate and the reduced growth of juvenile prawns at Henderson Inlet from July to September to plankton blooms. At the time of stocking in early July, water transparency was depressed by a plankton bloom (Figure 3). A 20% mortality occurred during the first 2 wk of July followed by a decrease in the mortality rate after the bloom subsided (Figure 6). During the same period prawns at Clam Bay showed an estimated 2% mortality as determined from semidaily pen examination.

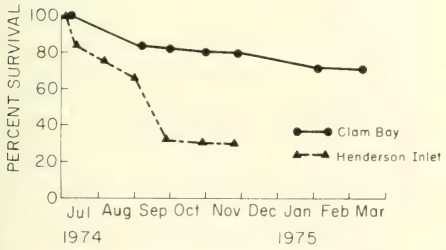


FIGURE 6.—Survival of juvenile spot prawns from July 1974 to March 1975 at Henderson Inlet and Clam Bay.

The mortality of juvenile prawns at Henderson Inlet increased again in early September during blooms of the dinoflagellates, *Ceratium* sp. and *Peridinium* sp. Salmon mortalities also increased in adjacent net pens during this period. Prawn mortalities at Henderson Inlet decreased with the end of the intense plankton blooms in the fall (Figures 3, 6).

Substantial mortalities of Pacific salmon reared in net pens in British Columbia have also been associated with algae blooms. Kennedy et al.[5] suggested that the algae promoted the production of suffocating mucus or physically damaged gills through contact with sharp diatom spicules. At Henderson Inlet the prawns' gills were noticeably blackened and had unidentifiable matter on the lamellae that may have been mucus or deteriorated dinoflagellates.

At Henderson Inlet, during the first 2 wk only, several dead prawns had single lesions—dark in the center and often surrounded by an area of reddish tissue. These lesions were not observed on the prawns at Clam Bay. Lightner and Lewis (1975) found the cuticular injuries from handling of penaeid shrimp resulted in bacterial septicemic diseases. Handling could partly explain the lesions and initial losses of juvenile prawns at Henderson Inlet because the net pens were pulled to the surface frequently to remove old food and dead prawns. This procedure was not followed at Clam Bay where water transparency allowed examination of the prawns in place.

Growth and Survival of Yearlings

No yearling prawns at Henderson Inlet survived in either dietary treatment after the first 2.5 mo (Figure 7). In early June, maximum surface temperatures increased from 11.8° to 21.9° C in 1 wk,

[5]Kennedy, W. A., C. T. Shoop, and W. Griffioen. 1975. Preliminary experiments in rearing Pacific salmon (1973 parr). Environ. Can., Fish. Mar. Serv., Tech. Rep. 541, 17 p. Pac. Biol. Stn., Nanaimo, B.C. V9R 5K6.

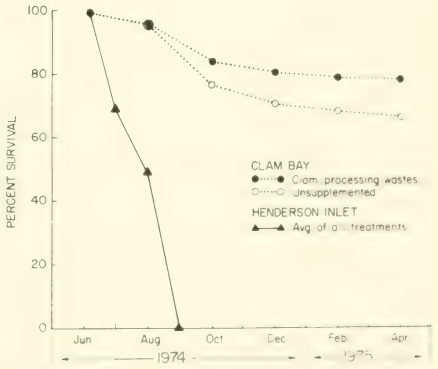


FIGURE 7.—Survival of yearling prawns held in floating net pens at Henderson Inlet and Clam Bay.

and the weekly mean rose about 5° C. As mentioned previously, a plankton bloom also occurred during this period. The rapid rise in water temperature and the onset of plankton blooms were the primary factors associated with the rapid rise in mortality rate of the yearling prawns. Abnormalities in appearance and behavior of the prawns were noted soon after their arrival at Henderson Inlet in June. The prawns became covered with fouling organisms, particularly the hydroid, *Obelia* sp., and the suctorian protozoan, *Ephelota gemmipara*. Heaviest fouling occurred on periopods and ventral edges of the cephalothorax, but the gills were unaffected. Within 2 wk many prawns were dying while survivors seemed lethargic and did not feed or molt. The entire stock was given a formaldehyde/malachite green dip (25 to 0.1 ppm ratio for 8 h), but beneficial effects lasted only a few days.

On 2 July, 49 surviving yearling prawns from one clam-fed replicate at Henderson Inlet were removed from the experiment and placed in a vinyl coated wire mesh cage ($0.9 \times 0.9 \times 0.5$ m) that was placed on the bottom of the Inlet, into water that was colder (Figure 2), less lighted, and out of the influence of the surface plankton bloom. Within 2 d the prawns became active and began molting although many still had some fouling organisms. By September, only four mortalities had occurred in the cage (92% survival), while prawns in the surface net pens had suffered 100% mortality. Colder water, reduced light, and the possibility of being out of the surface plankton bloom could explain this increase in survival. There are no natural populations of prawns in the shallow inlets of southern Puget Sound (i.e., those inlets to the west of Henderson Inlet). Berkley (1930) noted that late larval and postlarval prawns in British Columbia were commonly found inshore at depths of 3.7-5.5 m. The adverse conditions encountered in surface waters during this study produced extensive mortalities and could explain the absence of natural prawn populations in the shallow inlets of southern Puget Sound.

Survival of yearling prawns at Clam Bay after 10 mo (5 June 1974-28 March 1975) was 78.6% for clam-fed treatments and 66.7% for unsupplemented dietary treatments (Figure 7). The difference in survival was significant ($\chi^2 = 9.48$, df = 1, $P<0.005$).

Temperature fluctuations and plankton blooms at Clam Bay were associated with increases in mortality. Over half of the total mortalities occurred in a 2-mo period (August-September) in which the weekly mean temperature rose to a high for the year (14.2° C) and the lowest transparency value occurred (Figures 2, 3). In general, yearling prawn mortality coincided with rapidly decreasing water transparency and increasing water temperature and not the absolute value of Secchi disc readings.

Both treatment groups at Clam Bay grew at essentially the same rate during the June to August period. Thereafter the clam-fed prawns were significantly heavier ($t = 10.98$, df = 2,539, $P<0.00$) and longer ($t = 3.17$, df = 2,539, $P<0.001$) than the unsupplemented prawns (Figure 8).

Despite the fact that no food was given, the unsupplemented group had a positive growth rate throughout the experiment and a fairly high survival (66.7%). About 60% of prawns sampled at the termination of the experiment had materials in their stomachs, including unidentifiable brown matter, various algae (brown filamentous forms and diatoms, particularly *Riddulphia* sp.), and fragments of exoskeleton from either the prawns' exuviae or naturally occurring crustaceans in the net pens. The prawns had apparently maintained themselves on net fouling and/or pelagic organisms and through consumption of dead prawns or molted exuviae.

Net fouling organisms were preyed upon by prawns in both treatment groups. Commonly seen net fouling organisms (mussels, tunicates, and bryozoans) were noticeably absent from the nets containing prawns after 10 mo of immersion. The only major fouling organisms remaining were hydroids, *Obelia* sp., and small entroprocts (both

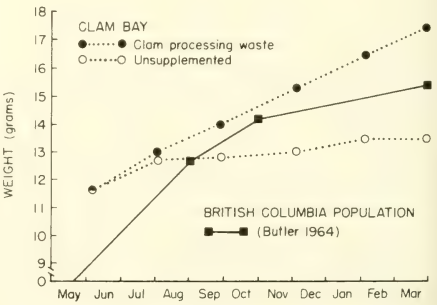


FIGURE 8.—Seasonal mean weight of yearling spot prawns reared at Clam Bay compared with a British Columbia wild population (Butler 1964).

restricted to the top 10 cm of the net). By feeding on net fouling organisms, the prawns not only make use of a free food supply, but they also provide net cleaning services that would reduce pen maintenance.

Molting

The yearling prawns held at Clam Bay showed five major molting peaks. At each peak, a higher percentage of clam fed prawns molted than unsupplemented prawns, but periods of peak molting generally coincided for each group (Figure 9). Two major molting peaks occurred in the summer about 50 d apart. By winter (November-February), the peaks were about 75 d apart, and by spring the intermolt periods were once again shortened to nearly 50 d. A pattern emerged with molting peaks occurring at either 1.6- or 2.5-mo intervals, depending on season. Rickards (1971) found a highly significant relationship between temperature and frequency of molting for tank-reared, juvenile pink shrimp, *Penaeus duorarum*. In the present study, the percentage of prawns molting appears related to temperature (Figure 9), but molt frequency is not related since it increases in late winter while water temperatures are still depressed. A previous study of juvenile prawns concludes that molt frequency decreases with age (Wickens 1972); however, there is no published account for molt frequency of older prawns. Kamiguchi (1971) reported that molt frequency of sexually immature *Palaemon pauciden* decreased with size until maturity when a constant interval between molting peaks was the rule.

In the present study, molting patterns may have been affected by changing photoperiod (Aiken 1969) and maturation as the prawns became functional males midway through the experiment.

In conclusion, surface waters of Henderson Inlet were unsuitable for prawn culture due to intense plankton blooms and rapid fluctuations of water temperature. These factors outweighed the growth stimulating effects of elevated water temperatures. Clam Bay was suitable for prawn culture although moderate mortalities were associated with plankton blooms and increases of water temperatures.

ACKNOWLEDGMENTS

This work was supported in part by the Washington Sea Grant Office and the Weyerhaeuser Company.

LITERATURE CITED

AIKEN, D. E.
1969. Photoperiod, endocrinology and the crustacean molt cycle. Science (Wash., D.C.) 164:149-155.

BERKELEY, A. A.
1930. The post-embryonic development of the common pandalids of British Columbia. Contrib. Can. Biol. Fish., New Ser. 6:79-163.

BRETT, J. R., AND J. E. SHELBOURN.
1975. Growth rate of young sockeye salmon, *Oncorhynchus nerka*, in relation to fish size and ration level. J. Fish. Res. Board Can. 32:2103-2110.

BUTLER, T. H.
1964. Growth, reproduction, and distribution of pandalid shrimps in British Columbia. J. Fish. Res. Board Can. 21:1403-1452.

CONKLEN, D. E.
1975. Nutritional studies of lobsters, *Homarus americanus*. *In* K. S. Price, Jr., W. N. Shaw, and K. S. Danberg (editors), First International Conference on Aquaculture Nutrition, p. 287-296. Univ. Del. Coll. Mar. Stud.

FORSTER, J. R. M.
1970. Further studies on the culture of the prawn, *Palaemon serratus* Pennant, with emphasis on the post-larval stages. Fish. Invest. Minist. Agric., Fish. Food (G.B.), Ser. II, 26(6), 40 p.

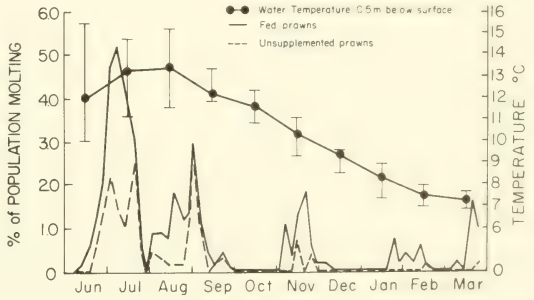


FIGURE 9.—Yearling spot prawn molting cycle 5-d means) and monthly means and ranges of surface water temperatures at Clam Bay.

KAMIGUCHI, T.
1971. Studies on the molting in the freshwater prawn, *Palaemon pauciden*. I. Some endogenous and exogenous factors influencing the intermolt cycle. J. Fac. Sci. Hokkaido Univ., Ser. VI, Zool. 18(1):15-23.

KELLY, R. O. A., A. W. HASELTINE, AND E. E. EBERT.
1976. Mariculture potential of the spot prawn, *Pandalus platyceros* Brandt. Aquaculture 10(1):1-16.

LIGHTNER, D. V., AND D. H. LEWIS.
1975. A septicemic bacterial disease syndrome of penaeid shrimp. Mar. Fish. Rev. 37(5-6):25-28.

MAHNKEN, C. V. W.
1975. Status of commercial-net pen farming of Pacific salmon in Puget Sound. Proc. 6th Annu. Meet. World Maricult. Soc., p. 285-298.

MAHNKEN, C. V. W., A. J. NOVOTNY, AND T. JOINER.
1970. Salmon mariculture potential assessed. Am. Fish Farmer 2(1):12-15, 27.

RENSEL, J. E., AND E. F. PRENTICE.
1977. First record of a second mating and spawning of the spot prawn, *Pandalus platyceros*, in captivity. Fish. Bull., U.S. 75:648-649.
1978. Growth of juvenile spot prawn, *Pandalus platyceros*, in the laboratory and in net pens using different diets. Fish. Bull., U.S. 76:886-890.

RICKARDS, W. L.
1971. Studies on the use of vertical substrates for improving production of pink shrimp, *Penaeus duorarum* Burkenroad. Univ. Miami Sea Grant, Tech. Bull. 10, 152 p.

WICKENS, J. F.
1972. Experiments on the culture of the spot prawn *Pandalus platyceros* Brandt and the giant freshwater prawn *Macrobrachium rosenbergii* (de Man). Fish. Invest. Minist. Agric., Fish. Food (G.B.), Ser. II, 27(5), 23 p.

REARING CONTAINER SIZE AFFECTS MORPHOLOGY AND NUTRITIONAL CONDITION OF LARVAL JACK MACKEREL, *TRACHURUS SYMMETRICUS*

Container size may be a critical variable in the rearing of marine fish larvae. Northern anchovy, *Engraulis mordax*, grew faster in 500 l than in 10 l containers (Theilacker and McMaster 1971), and Blaxter (1976) suggested that growth of laboratory-reared fish may depend on space available in tanks as well as food supply and fish density. On intuitive grounds, large containers are preferable for rearing studies but small containers are often used because fewer food organisms are required, treatments can be replicated easily, and daily mortality can be easily monitored. Thus, information is needed on the extent container size affects results of laboratory studies on marine larvae. In this paper, I compare the growth, morphology and nutritional condition of jack mackerel, *Trachurus symmetricus*, larvae reared in 10 l and 100 l containers.

Methods

I collected jack mackerel eggs by towing a 1 m (0.505 mm mesh) plankton net just below the sea surface 61 km off southern California in May 1976. Sea surface temperature was 15.3° C. I sorted and staged normally developing eggs from the plankton and stocked eggs of the same stage at 5/l into 10 l and 100 l black circular rearing containers containing 5 μm filtered seawater at 15.0° C and a light cycle of 12 h light and 12 h dark. I used two treatments for each container size, one fed and the other unfed. Data from the 100 l treatments were reported earlier (Theilacker 1978). Larval diet consisted of a naked dinoflagellate, *Gymnodinium splendens* (50/ml), a rotifer, *Brachionus plicatilis* (30-40/ml), and a copepod, *Tisbe* sp. (1-2/ml). This feeding method has been described previously (Lasker et al. 1970; Theilacker and McMaster 1971; Hunter 1976).

Larvae began to eat 5 d after hatching. I sampled 5-30 larvae daily from fed and starved treatments beginning on day 6 and preserved the larvae in Bouin's solution. Four to five weeks after preservation, I measured standard length (SL, tip of upper jaw to perpendicular at end of notochord), head length (HL, tip of upper jaw to cleithrum), eye diameter (ED), body depth at the pectoral fin (BD-1), and body depth at the anus (BD-2). Shrinkage of jack mackerel body parts in Bouin's solution was as follows: SL, 8%; HL, 18%; ED, 10%; BD-1 and BD-2, 25% (Theilacker 1980). (Data in Table 1 are preserved measurements.) After measurement, I used standard techniques (Theilacker 1978) to prepare larvae for histological examination.

I examined the tissue microstructure of all larvae in fed and starved treatments to determine whether larvae were eating or starving. The onset of starvation in jack mackerel larvae is characterized by a change in the acinar arrangement of pancreatic cells and a sloughing of mucosal cells from the midgut into the lumen (Theilacker 1978). I graded these characteristics of the pancreas and gut and classified individual larval nutritional condition as "healthy," "intermediate," or "starved" (Theilacker 1978). Because histological assessments of larval condition are based on tissue microstructure, these assessments are independent of larval size.

Results

Diameter of jack mackerel eggs collected for this study averaged 1.0 mm. Larvae hatched at 2.45 mm SL (preserved) on day 0 and began to eat at 3.35 mm SL at age 5 d when most yolk was absorbed.

Fed larvae were larger in 100 l than in 10 l containers on each day after the onset of feeding (day 5), but statistically significant differences in size among larvae in the large and small containers did not occur until the larvae had fed for 4 d, age 9 d ($P = 0.002$; Hotelling T^2 multivariate analysis; Table 1).

Among groups receiving no food, larvae in 10 l containers were larger than those starved in 100 l containers at age 8 d, third day of starvation ($P = <0.001$; Hotelling T^2 multivariate analysis; Table 1.) Also, starved larvae in small containers survived 2 d longer than those in large containers, 10 d versus 8 d.

Nutritional condition of fed larvae reared in 10 l and 100 l containers was similar for 5 feeding days,

TABLE 1.—Daily mean body measurements of fed and starved jack mackerel larvae maintained in 10 l and 100 l containers.

Body parts[1]	Day 6				Day 7				Day 8				Day 9				Day 10				Day 11	
	10		100		10		100		10		100		10		100		10		100		10	
	mm	SD	mm	SD	mm	SD	mm	SD	mm	SD	mm	SD	mm	SD	mm	SD	mm	SD	mm	SD	mm	SD
FED																						
Standard length	3.30	0.16	3.35	0.11	3.43	0.05	3.48	0.13	3.38	0.19	3.56	0.13	3.37	0.13	3.83	0.24	3.35	0.21	3.72	0.20	3.35	0.15
Head length	.67	.03	.70	.03	.73	.02	.74	.04	.73	.05	.77	.03	.71	.03	.85	.06	75	.07	85	07	.76	.06
Eye diameter	.23	.02	.25	.02	26	.01	26	.01	.26	.02	.29	.02	.25	.02	32	.02	27	02	.31	.03	.25	.01
Body depth-1	40	.02	43	.11	48	.03	.48	.03	.48	.04	.52	.04	48	.04	.59	.04	46	.06	.58	06	.47	.03
Body depth-2	.18	01	20	.05	.19	.01	.20	02	.19	.02	.22	.02	.19	.02	.25	.01	.20	.02	.23	.02	.18	.01
n	4		15		5		15		5		15		5		10		17		15		7	
^2P	0.463				0.523				0.109				0.002				0.001					
STARVED																						
Standard length			3.31	0.11	3.27	0.15	3.35	0.13	3.29	0.12	3.04	0.17	2.99	0.33			3.07	0.21				
Head length			.66	.04	68	.03	.69	.02	71	.03	.64	.04	65	.04			.66	.05				
Eye diameter			.24	.02	.24	.02	25	.01	.24	.02	.23	.01	24	.01			.25	.02				
Body depth-1			.41	.03	40	.03	.42	.02	38	.02	.42	.03	.36	.02			.35	.02				
Body depth-2			.18	.02	.18	.01	.18	.01	.17	01	.17	.01	.17	.01			.17	.01				
n			14		28		15		15		19		16				26					
^2P					0.351				<0.001													

[1] Preserved measurements.
[2] Probabilities for equal body measurements between container sizes (multivariate analysis; Hotelling T^2)

TABLE 2.—Daily histological condition of fed and starved jack mackerel larvae maintained in 10 l and 100 l containers.

Histological grade[1]	FED											STARVED						
	Day 6		Day 7		Day 8		Day 9		Day 10		Day 11	Day 6	Day 7		Day 8		Day 9	Day 10
	10	100	10	100	10	100	10	100	10	100	10	100	10	100	10	100	10	10
Starved (1.00-1.66)	0	1	0	0	1	1	1	1	8	1	3	7	20	6	12	15	8	22
Intermediate (1.67-2.33)	3	1	0	2	0	3	0	0	4	2	0	3	3	6	0	1	1	2
Healthy (2.34-3.00)	1	12	5	13	3	11	4	9	4	12	3	3	1	2	0	2	0	0
Average grade	2.25	2.77	2.90	2.80	2.50	2.62	2.60	2.80	1.80	2.65	2.08	1.88	1.32	1.71	1.00	1.25	1.11	1.08
^2n	4	14	5	15	4	15	5	10	16	15	6	13	24	14	12	18	9	24
^3P	>0.10		>0.10		>0.10		>0.10		>0.05			>0.10			>0.10			

[1] Theilacker (1978).
[2] Total number of larvae within each treatment does not agree with Table 1, as several larvae were lost during the microtechnique procedure.
[3] Probabilities for equal histological grades between container sizes (two-sample nonparametric Kolmogorov-Smirnov Test).

until age 10 d when it was significantly better in the large containers ($P = <0.05$; Kolmogorov-Smirnov Test; Table 2); fewer larvae were classed as "starved" in the larger containers. For larvae given no food, no difference existed in condition of larvae between large and small containers.

Fed larvae died at ages 12-13 d in the small containers. On day 13 there was also a major mortality in the large containers, but a few larvae survived through the juvenile stage, and one fish lived for 49 d, 31 mm SL. I did not sample these survivors unless they appeared to be dying. For jack mackerel there is no well-defined metamorphosis; the juvenile stage begins at the completion of fin formation, 12-16 mm (Ahlstrom and Ball 1954). In the large container, fin formation was complete at 14 mm, 39 d of age ($n = 1$); size at age for this laboratory-reared fish was similar to field-collected fish (age of wild fish is being determined by reading daily growth increments in otoliths (Methot[1])).

Conclusions

Relating experimental results from laboratory to field conditions must be done with caution. Blaxter (1975) compared morphology, chemistry,

[1] R. Methot, Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun. January 1980.

and physiology between reared and wild larvae and concluded that results on growth, nutrition, and mortality of laboratory-reared larvae should not be related to the field. My study shows that jack mackerel larvae reared with food in 10 l containers were smaller and in poorer nutritional condition than larvae reared in 100 l containers. These container-effects occurred at an early age, i.e., morphological differences were evident 9 d after hatching and histological differences 10 d after hatching. Larvae may grow faster and show fewer signs of starvation in large containers because: 1) there is a lower probability of damage from contact with the walls; and/or 2) the same prey density in a larger container may permit the formation of larger food patches and thereby elevate the actual density of food encountered by the larvae; and/or 3) water chemistry in larger containers may be more favorable.

In contrast to results of the feeding experiments, larvae starved in 10 l containers survived 2 d longer and were larger at age 8 d than those in 100 l containers. This indicates that activity may be affected by container size. Larvae in small containers may be less active, consume energy reserves less rapidly, and therefore live longer without food.

The effect of container size on growth, nutritive condition, and possibly activity in jack mackerel larvae, emphasizes the caution that must be exercised when relating results from laboratory to field conditions. The large container may have had no effect on growth and development of jack mackerel, but survival was poor. Further studies are needed to determine the minimum container size required to simulate natural conditions in the laboratory. Because spatial requirements of larval fish depend on locomotory patterns as well as on genetic adaptations to life near solid surfaces (Kinne 1977), optimum container size will probably vary with fish species. In larval fish experiments, container size is a variable that must be considered with temperature, light, food type and availability, and stocking density.

Acknowledgments

Thanks to John Hunter and two anonymous reviewers for critically reviewing the manuscript, Jack Metoyer for helping me measure larvae, Susan Picquelle for helping with the statistical analyses, Kate Coleman for typing the draft and tables, and Lorraine Prescott for final typing.

Literature Cited

AHLSTROM, E. H., AND O. P. BALL.
1954. Description of eggs and larvae of jack mackerel (*Trachurus symmetricus*) and distribution and abundance of larvae in 1950 and 1951. U.S. Fish Wildl. Serv., Fish. Bull. 56:207-245.

BLAXTER, J. H. S.
1976. Reared and wild fish—how do they compare? Proc. 10th Eur. Symp. Mar. Biol. 1:11-26.

HUNTER, J. R.
1976. Culture and growth of northern anchovy, *Engraulis mordax*, larvae. Fish. Bull., U.S. 74:81-88.

KINNE, O.
1977. Pisces: Rearing of larvae. *In* O. Kinne (editor), Marine ecology, Vol. 3, p. 968-1004. Wiley, N.Y.

LASKER, R., H. M. FEDER, G. H. THEILACKER, AND R. C. MAY.
1970. Feeding, growth, and survival of *Engraulis mordax* larvae reared in the laboratory. Mar. Biol. (Lond.) 5:345-353.

THEILACKER, G. H.
1978. Effect of starvation on the histological and morphological characteristics of jack mackerel, *Trachurus symmetricus*, larvae. Fish. Bull., U.S. 76:403-414.
1980. Changes in body measurements of larval northern anchovy, *Engraulis mordax*, and other fishes due to handling and preservation. Fish. Bull., U.S. 78:685-692.

THEILACKER, G. H., AND M. F. MCMASTER.
1971. Mass culture of the rotifer *Brachionus plicatilis* and its evaluation as a food for larval anchovies. Mar. Biol. (Berl.) 10:183-188.

GAIL H. THEILACKER

Southwest Fisheries Center La Jolla Laboratory
National Marine Fisheries Service, NOAA
P.O. Box 271
La Jolla, CA 92038

EFFECTIVENESS OF METERING WHEELS FOR MEASUREMENT OF AREA SAMPLED BY BEAM TRAWLS

It was the purpose of this study to evaluate the effectiveness of using an odometer wheel to measure distance sampled by a trawl. A 3 m beam trawl has been used extensively in a series of benthic ecology studies off the coast of Oregon at depths ranging between 50 and 4,000 m. Two odometer wheels were attached to the trawl in an attempt to measure the distance covered during sampling. The effectiveness of the odometers was examined statistically from performance data collected during 337 hauls over a 3,950 m depth range. In spite of repeated use and repeated suggestions as to the usefulness (Holme and McIntyre 1971; Menzies et al. 1973) there have been no

critical evaluations and few reports of faunal density specifically attributed to odometer wheels (Belyaev and Sokolova 1960; Pearcy 1972; Carey et al. 1973; Bieri 1974a, b).

Methods

Analysis consisted of comparisons of the actual wheel performance with the performance expected of the wheels if working as designed. We were concerned with accuracy and precision. Did the wheels actually measure the distance towed, and how much random variation was there in the wheel counts? Exacting answers to these questions would have required a careful calibration of the wheels under conditions encountered in sampling at various depths. Such a deep-sea calibration would have required more effort than the subsequent ecological sampling. However, partial answers were obtained through the examination of data collected during extensive ecological sampling.

As the trawl was dragged along bottom, the wheels should have rotated with the rotations counted on the hub odometers. Due to friction in the wheel mounts and poor consolidation of the sediment, each wheel slipped some portion of the distance dragged. Thus the wheel counts should have normally underestimated the distance actually towed. We are confident that the wheels did not rotate while in the water column because in those accidental cases where the trawl failed to reach bottom, <10 rotations were registered. On a single haul variation in slippage caused the left and right wheel to register different counts. However, even if biased, the wheel counts should have shown three relationships. First, wheel counts should have been positively correlated with other estimates of distance based on navigational fixes and towing times. Second, the ratios of wheel counts accumulated from all hauls should have provided information on the magnitude of the variation between wheels due to small-scale sediment changes and operational characteristics. Third, if sampling occurred within an area of faunal uniformity, catch size might have been related to wheel count. However, since catch was also determined by the actual, usually patchy, faunal distribution, the absence of positive correlation can not be taken as unequivocal evidence that the wheels did not function as designed.

Estimates of distance sampled based on changes in loran A position or speed × duration of tow are subject to major random error. In either case the greatest error component is that associated with determining the precise moment the trawl is on and off bottom. Additionally loran A fixes contain an inherent technical error, and speed × duration estimates are dependent upon accurate determinations of true speed over bottom. Since both of these distance estimates were subject to random error, correlation was the appropriate method of comparison. The raw data were critically examined to remove as much obvious misinformation as possible. If the distance by loran was greater than it was possible for the ship to have gone given speed and current conditions, the tow was excluded. The greatest source of loran A error seems to have been simple operator error yielding tow distances that were far too great.

The beam trawl was made of a thick-walled, hollow aluminum tube bolted across the top of two steel skids. The skids were lined with netting, and an otter trawl type net attached to the trailing edge of the skids (Figure 1). The basic configuration and full operating details have not changed since the initial report by Carey and Heyamoto (1972). This beam trawl had many similarities to those used for fishing since the 16th century (Davis 1958). The bicycle wheels of an earlier version of the trawl were replaced by heavier, spiked aluminum disks to decrease damage to the wheels during launch and recovery and while on bottom. A Veeder Root[1] model 54-794692 (Veeder Root Corp., Hartford, Conn.) hub odometer was attached to the axle of each wheel, counting once each revolution (2 m distance). The counter was housed in a thick-walled brass case filled with silicon fluid to prevent air spaces which might lead to crushing at high hydrostatic pressures. The wheel and its mounting fork were attached to the outside of each skid, free to pivot about the mounting bolt. Surgical tubing was used to restrict the angle of swing. Short lengths of angle iron were welded to the bottom of the skids in front of the wheels. These were intended to protect the wheels and to prevent rotation while off bottom. The trawl was paid out at a ship's speed through water of approximately 2 kn. No weights were placed on the bridle or towing line. The time of bottom contact was estimated by an empirically determined table of wire-out needed to reach bottom. A Benthos model 1170 (Benthos Corp., Falmouth,

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

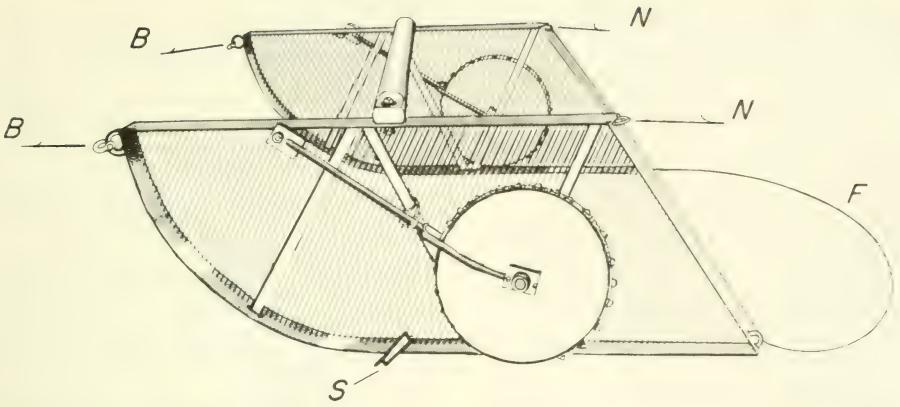


FIGURE 1.—Skid and beam portion of the beam trawl. The towing bridle is attached to the upper leading edge of each skid (points B). The headline is attached to points N. The lateral angle iron extensions (S) are intended to act as stops to prevent wheel turning when off bottom. The skids are lined with netting (hatched areas). The main net is not shown, but the footline is represented by F.

Mass.) time-depth recorder was attached to the trawl, but was lost after only 17 trials.

Results

Consistency of the Two Wheel Counts

Wheel count ratios ranged over a wide span of values. However, there was good agreement between the wheels on about 50% of the hauls (Figure 2) with a ratio of 1.105 or less, and 83% of the ratios were <2.000. Even though the histogram of ratios showed that close agreement between wheels was more common than poor agreement, it was difficult to determine the normal range of random variation. A high ratio might have been due to inherent variation or to mechanical failure of one of the wheels. A wheel might have recorded

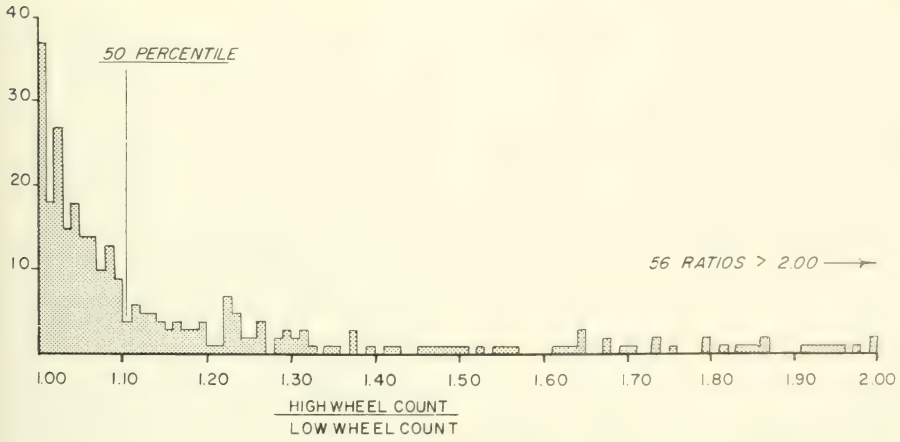


FIGURE 2.—Frequency of occurrence of high:low wheel count ratios, $n = 337$.

a very low count because it was fouled on the net or jammed against the frame during some portion of the tow, but have been in apparently good working order when retrieved. For consistency during subsequent analyses, all ratios >2.000 were considered to be due to a malfunction of one wheel causing a very low reading for the possible distance towed. We feel that this cut off was justified on the basis of the shape of the histogram of ratio frequencies (Figure 2). Seventeen percent of all hauls fell into this malfunction category. The remaining 33% of ratios, between 1.105 and 2.000, represented a high level of normal operational variation. In all cases of ratios >2.000 it was an unusually low wheel reading which produced the high ratio, not an unusually high one. Ratios >2.000 were not further considered in the analyses.

Consistency with Other Estimates of Distance

Wheel counts were significantly positively correlated (95% level) with time duration and loran determined estimates of distance (Table 1), but the correlations were not high. Much more precise estimates of time duration distances were available on the 17 tows employing a time-depth gage. All the gaged hauls were taken between 2,500 m and 3,000 m where bottom conditions were relatively uniform. The correlations between the wheel counts and distance based on gage time on bottom were significant (+0.89 at the 95% level) and much higher than with wire-out determined values. This marked improvement in correlation indicates that errors in determining actual bottom contact time were the major source of difference between wheels and other measures of distance.

The 17 time-depth gage records were compared with the wire-out time on bottom estimates. On average the trawl was actually on bottom 23 min longer than predicted, varying from 75 min longer to 65 min shorter.

The time-depth gage readings were also used to determine a rough estimate of the amount of wheel slippage. Using linear regression the gage measurement of bottom time was taken as the independent variable and the wheel counts as the dependent variable. If the average speed over bottom was the intended 2.0 kn, and if no slippage occurred, then the slope of regression should have been 30.85 (counts per minute). While significantly different from zero, the slope of regression (19.2) was also significantly lower than the expected 30.85 at the 95% level. This major discrepancy may have been due to a ship's speed over bottom consistently much less than 2.0 kn, considerable wheel slippage, or both. If ship's speed over bottom actually did average 2 kn, then an estimate of the worst slippage was 40%. If the ship's speed was consistently low, then the wheels performed better by slipping less.

TABLE 1.—Correlation coefficients between measurements of distance towed. All values are significantly greater than 0.0 (95% level). Asterisk denotes values significantly higher in selected data. Significance was tested following z-transformation. Data selection consisted of removing exceedingly large position changes and samples with a wheel ratio >2.0 (see text).

		Selected data n = 257		
Item	Position	Time	High wheel	Low wheel
Raw data n = 337:				
Position		0.529*	0.638*	0.628*
Time	0.370		544	515
High wheel	.183	.591		.972*
Low wheel	.181	.551	809	

Wheel Counts Versus Catch Data

No consistent positive relationships were found between the catch of the trawl and the wheel count estimates of distance. This lack of the desired positive correlation was difficult to evaluate because catch was controlled by performance of the trawl and the actual distribution of the fauna. Faunal variation among areas sampled may have masked variation in catch due to differences in distance towed.

In one comparison the echinoderm catch of 22 pairs of consecutive tows in approximately the same bottom area at continental shelf depths was examined. According to wire-out determinations of time on and off bottom all 44 tows were on bottom 20 min. Echinoderm catch was considered because these asteroids, echinoids, and holothuroids represent relatively immobile large benthic organisms. The number of species and total specimens were taken separately as measures of catch size. The number of times the longer haul of the pair (as indicated by the magnitude of the low wheel count on each sample) had the greatest catch was tallied for all pairs of samples and compared against random expectations using a nonparametric sign test (Table 2). While having a greater catch in most cases, the longer tows did not take significantly higher numbers of echinoderm species or specimens.

In addition we examined the catch of the abun-

TABLE 2.—Nonparametric sign test of catch sizes for selected echinoderms in 22 pairs of samples. The long haul in each pair was that with both wheel counts being greater than both wheel counts of the other sample in the pair. When the counts overlapped, the pair was excluded since there was no unambiguous longer or shorter haul. All sample pairs were taken at the same locality on the same day.

Criterion	Highest value in		Significance ($P \leq 0.05$)
	Long haul	Short haul	
Most echinoderm species	15	7	ns
Most echinoderm specimens	16	6	ns

dant megafaunal holothuroids off Oregon at 2,500-3,000 m. The catches for each species were compared with the wheel count estimates of distance towed (based on the average of the two wheels) by computing correlation coefficients. According to wire-out determinations all of these tows were on bottom 120 min. These coefficients were computed with the zero holothuroid catches included and then with zero catches excluded (Table 3). There was no consistent pattern of positive correlation.

TABLE 3.—Correlation of number of specimens of each species of holothuroid with distance on bottom sampled as determined by wheel counts (see text). Correlation coefficients were computed for each species over all samples ($n = 100$) and for only those samples where the species was taken (zeros excluded) to reduce the effects of possible aggregation.

Species	Correlation		No. of hauls	No. of specimens
	All hauls	Zero catch excluded		
Paelopatides confundens	0.043	0.034	90	5,857
Peniagone cf. *dubia*	0.205*	0.201	79	6,133
Scotoplanes globosa	0.044	0.045	75	4,521
Psychropodes longicaudata	0.210*	0.177	68	396
Molpadia musculus	0.011	0.011	33	85
Pseudostichopus nudus	0.061	−0.191	22	48

*$P < 0.05$

Discussion

The earliest reported use of odometer wheels was by Bieri and Bradshaw (cited in Gunther 1957) whose system evolved into a more sophisticated opening and closing quantitative trawl (Bieri and Tokioka 1968). Subsequently, Belyaev and Sokolova (1960), Riedl (1961), Gilat (1964), Richards and Riley (1967), Pequegnat et al. (1970), and Carey and Heyamoto (1972) reported the use of similar devices. Additionally, Wolff (1961) presented a photograph attributed to Zenkevitch of a Soviet beam trawl carrying four odometer wheels similar to those discussed in this report.

Positive correlation between counts, duration, and position change is supportive of the basic contention that the wheels can provide a measure of the distance sampled. However, major questions remain as to the accuracy and precision of the wheels, and the relationship between estimates of area sampled and the catch results. It must be stressed that the positive correlation among distance estimates does not mean that they are either accurate or precise. Our regression of the limited time-depth bottom time estimates on odometer readings indicated that the wheels were inaccurate, being biased by as much as 40% below the actual distance. The numerous low wheel count ratios indicated that the wheels did produce relatively low variance measurements most of the time.

Photographic evidence indicated that the lack of a positive correlation between catch and wheel count might have been due to irregularities that affected total trawl performance, not just the operation of the wheels. Using a camera mounted to the trawl frame it was determined that during a portion of each haul the trawl skids rocked forward, lifting the footline of the net off bottom. The odometer wheels, however, remained in contact with the bottom registering the distance towed. The severe saltations observed by Rowe and Menzies (1967) and Menzies et al. (1973) were not observed in these photographs and did not appear to be a problem with the beam trawl used in this study.

The failure of the footline to constantly tend bottom does not detract from the usefulness of odometer wheels, but it does make it difficult to interpret faunal data in terms of density (Pearcy 1978). Nevertheless, in some preliminary comparisons of trawl versus photographic determinations of faunal densities good agreement has been found. Pearcy (1972) measured populations of the pink shrimp, *Pandalus jordani*, at shelf depths using both techniques and got similar estimates of about 10 individuals/m^2. Similarly Carey et al.[2] measured ophiuroid densities at about 2,500 m and got similar estimates of 2 or 3 specimens/m^2.

Conclusions

The system of trawl frame and odometer wheels used in this study did not produce estimates of

[2]Carey, A. G., Jr., J. Rucker, and R. Tipper. 1973. Benthic ecological studies of deepwater dumpsite G in the northeast Pacific Ocean off the coast of Washington. *In* Proceedings of the First Conference of the Environmental Effects of Explosives and Explosions (May 30-31, 1973), p. 120-137. Nav. Ord. Lab. Tech. Rep. 73-32, N.O.R.D.A., Bay St. Louis, MS 39520.

distance towed which could be used without reservation to estimate the density of fauna. The positive correlation between wheel counts and two other distance measures indicate that the wheels do reflect distance. However, there is so much uncertainty concerning accuracy and precision that it is impossible to decide if apparent faunal density variation is real or an artifact. The real potential of bottom measuring wheels lies in the fact that they are simple, inexpensive, as trawl equipment. For certain sampling problems trawls will remain the sampler of choice. If wheels can be improved then trawl data can be quantified with greater confidence. Future development should focus upon improved precision and a method of field calibration to determine accuracy.

Acknowledgment

We gratefully acknowledge the financial support of the Biological Oceanography Program of the National Science Foundation grant GB-4629; the former Atomic Energy Commission contracts AT(45-1) and AT(45-1)2227; and the National Oceanic and Atmospheric Administration Institutional Sea Grant 2-5187. Ship usage was partially supported by National Science Foundation grant OCE-7600061. The Department of Energy reference for this manuscript is RLO-227-T12-72. R. Ruff, M. Kyte, and R. Paul contributed to the design of the beam trawl. W. Pearcy, D. Cohen, M. Downey, and anonymous reviewers gave helpful guidance during writing.

Literature Cited

BELYAEV, G., AND M. SOKOLOVA.
1960. K voprosu o metodikye kolichestvennie issledovanii glubokovodnogo bentosa [On the issue of quantitative methods of investigation of deep-sea benthos]. [In Russ.] Tr. Inst. Oceanol. 39:96-101.

BIERI, R.
1974a. A new species of *Spadella* (Chaetognatha) from California. Publ. Seto Mar. Biol. Lab. 21:281-286.
1974b. First record of the chaetognath genus *Krohnittella* in the Pacific and description of a new species. Wasmann J. Biol. 32:297-301.

BIERI, R., AND T. TOKIOKA.
1968. Dragonet II, an opening-closing quantitative trawl for the study of microvertical distribution of zooplankton and the meio-epibenthos. Publ. Seto Mar. Biol. Lab. 15:373-390.

CAREY, A. G., JR., AND H. HEYAMOTO.
1972. Techniques and equipment for sampling benthic organisms. *In* A. T. Pruter and D. L. Alverson (editors), The Columbia River estuary and adjacent ocean waters; bioenvironmental studies, p. 378-408. Univ. of Wash. Press, Seattle.

DAVIS, F. M.
1958. An account of the fishing gear of England and Wales. Fish. Invest. Minist. Agric. Fish. Food (G.B.), Ser. II, 21(8), 165 p.

DIXON, W. J., AND F. J. MASSEY, JR.
1969. Introduction to statistical analysis. 3d. ed. McGraw-Hill, N.Y. 638 p.

GILAT, E.
1964. The macrobenthonic invertebrate communities on the Mediterranean continental shelf of Israël. Bull. Inst. Oceanogr. Monaco 62 (1290), 46 p.

GUNTHER, G.
1957. Dredges and trawls. *In* J. Hedgpeth (editor), Treatise on marine ecology and paleoecology. Vol. 1, p. 73-78. Geol. Soc. Am. Mem. 67.

HOLME, N. A., AND A. D. MCINTYRE (editors).
1971. Methods for the study of marine benthos. IBP (Int. Biol. Programme) Handb. 16, 334 p.

MENZIES, R. J., R. Y. GEORGE, AND G. T. ROWE.
1973. Abyssal environment and ecology of the world oceans. Wiley, N.Y., 448 p.

PEARCY, W. G.
1972. Distribution and diel changes in the behavior of the pink shrimp, *Pandalus jordani*, off Oregon. Proc. Natl. Shellfish. Assoc. 62:15-20.
1978. Distribution and abundance of small flatfishes and other demersal fishes in a region of diverse sediments and bathymetry off Oregon. Fish. Bull., U.S. 76:629-640.

PEQUEGNAT, W. E., T. J. BRIGHT, AND B. M. JAMES.
1970. The benthic skimmer a new biological sampler for deep-sea studies. *In* W. E. Pequegnat and F. A. Chase, Jr. (editors), Contributions on the biology of the Gulf of Mexico, p. 17-20. Tex. A&M Univ. Oceanogr. Stud. 1.

RICHARDS, S. W., AND G. A. RILEY.
1967. The benthic epifauna of Long Island Sound. Bull. Bingham Oceanogr. Collect. Yale Univ. 19:89-135.

RIEDL, R.
1961. Etudes des fonds vaseux de l'Adriatique. Méthodes et résultats. Recl. Trav. Stn. Mar. Endoume 23: 161-169.

ROWE, G. T., AND R. J. MENZIES.
1967. Use of sonic techniques and tension records as improvement in abyssal trawling. Deep-Sea Res. 14: 271-272.

WOLFF, T.
1961. Animal life from a single abyssal trawling. Galathea Rep. 5:129-162.

ROBERT S. CARNEY

Department of Invertebrate Zoology
U.S. National Museum
Smithsonian Institution
Washington, DC 20560

ANDREW G. CAREY, JR.

School of Oceanography
Oregon State University
Corvallis, OR 97331

STOMACH CONTENTS AND FECES AS INDICATORS OF HARBOR SEAL, *PHOCA VITULINA*, FOODS IN THE GULF OF ALASKA

Traditional methods of investigating pinniped feeding habits have involved examination of stomach contents from collected animals (Imler and Sarber 1947; Spalding 1964; Fiscus and Baines 1966). Recently, several scientists (Ainely et al.[1]; Calambokidis et al.[2]) have used scats collected from haulouts to study prey utilization of the California sea lion, *Zalophus californianus*, and the harbor seal, *Phoca vitulina*. This technique may be valuable in situations where killing animals is not feasible or desirable. No comparative information has been available for relating the results of scat analysis to stomach content analysis. Between 1975 and 1978 I identified food remains in stomachs and in feces from 351 harbor seals collected along the Gulf of Alaska coast from Yakutat Bay to Kodiak Island and was able to compare the data resulting from both sources. The sample of seals included both sexes and spanned all age-classes. Seals were collected during all months except December and January.

Methods

Seals were collected by shooting. Stomach contents were removed in the field, wrapped in muslin and preserved in a 10% Formalin[3] solution. Fecal material from large intestines was washed through nested sieves (2.00 and 0.84 mm²) and identifiable materials were recovered and preserved in 70% ethanol. Identifications of prey from both stomach contents and feces were based primarily on fish otoliths, cephalopod (squid and octopus) beaks and shrimp exoskeletons; occasionally vertebrae, preopercular bones, and intact specimens found in stomachs also were used. All otolith identifications were verified by John E. Fitch, California Department of Fish and Game, Long Beach.

Findings were compared by percentage of occurrences (number of stomachs or large intestines in which a prey species was found) in the stomach and fecal samples.

Results and Discussion

Spearman rank correlation analysis showed a significant positive correlation ($r_s = 0.79, P<0.01$) between the rankings of prey occurrences from stomach contents and feces (Table 1). The greatest discrepancy in rankings was for cephalopods which were ranked second in the analysis of stomach contents and ninth in the fecal analysis.

Occurrences of individual prey categories from stomach contents and feces showed good agreement when analyzed with contingency tables (Table 1). Only one significant statistical difference ($P<0.01$) was found among 10 testable categories. Cephalopods occurred more frequently ($P<0.001$) in stomach contents than in feces. The χ^2 value for cephalopods was so high (34.76) that rejection of the null hypothesis seemed justified even in light of potential type I errors resulting from multiple tests.

Cephalopods were identified primarily by their chitinous beaks in both stomach contents and feces. Beaks that were recovered in fecal material, although sometimes fragmented, were easily recognized. Apparently most beaks were regurgitated rather than passed through the intestinal tract. Captive northern fur seals, *Callorhinus ursinus*, which had been fed squid were observed regurgitating beaks (Miller[4]). Miller observed that the beaks appeared to be "trapped" in the stomach and were regurgitated at about 2-d intervals. This is probably also true in harbor seals as I have occasionally seen "wads" of beaks packed into the pyloric ends of stomachs. This would tend to exaggerate utilization of cephalopods in stomach contents if the beaks persisted longer than remains of other prey. Therefore cephalopods are apparently substantially underrepresented in feces and probably somewhat overrepresented in stomach contents.

[1]Ainley, D. G., H. R. Huber, R. R. LeValley, and S. H. Morrel. 1978. Studies of marine mammals at the Farallon Islands, California, 1976-77. Final report for MMC contract MM6AC027. Available National Technical Information Service, 5285 Port Royal Road, Springfield, VA 22151 as PB-286 603, 48 p.

[2]Calambokidis, J., K. Bowman, S. Carter, J. Cubbage, P. Dawson, T. Fleischner, J. Schuett-Hames, J. Skidmore, and B. Taylor. 1978. Chlorinated hydrocarbon concentrations and the ecology and behavior of harbor seals in Washington State waters. The Evergreen State Coll., Processed Rep., 121 p.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[4]Miller, L. K. 1978. Energetics of the northern fur seal in relation to climate and food resources of the Bering Sea. Final report for MMC contract MM5AC025. Available National Technical Information Service, 5285 Port Royal Road, Springfield, VA 22151 as PB-275 296, 32 p.

TABLE 1.—Comparative frequency of major prey identified in stomach contents and feces from 351 harbor seals collected in the Gulf of Alaska. Prey are ranked in descending order of occurrence. Comparisons of proportion of occurrence of prey found in stomach contents and feces were made by contingency table analysis when samples were adequate (minimum cell size ≥5).

	Stomach			Feces			
		Occurrences			Occurrences		
Prey	Rank	No.	%	Rank	No	%	χ^2
Walleye pollock, *Theragra chalcogramma*	1	80	24.8	1	104	35.9	4.24
Cephalopods, squids and octopus	2	68	21.1	9	8	2.8	34.76*
Capelin, *Mallotus villosus*	3	33	10.2	2	33	11.4	0.00
Flatfishes, Pleuronectidae	4	21	6.5	4	21	7.2	0.00
Pacific herring, *Clupea harengus pallasi*	5.5	20	6.2	3	24	8.3	0.39
Pacific cod, *Gadus macrocephalus*	5.5	20	6.2	6	17	5.9	0.26
Pacific sand lance, *Ammodytes hexapterus*	7	15	4.7	5	7	2.4	3.00
Pacific sandfish, *Trichodon trichodon*	8	10	3.1	10	19	6.6	2.91
Shrimps	9	7	2.2	14	4	1.4	—
Sculpins, Cottidae	10	6	1.9	7	14	4.8	3.29
Eelpouts, *Lycodes* spp.	11	5	1.6	10	7	2.4	0.34
Salmon, *Oncorhynchus* spp	13	4	1.2	15	0	0.0	—
Eulachon, *Thaleichthys pacificus*	13	4	1.2	13	5	1.7	—
Rockfishes, *Sebastes* spp.	13	4	1.2	10	7	2.4	—
Greenlings, *Hexagrammos* spp	15	2	0.6	12	6	1.2	—
Others[1]		23	7.1		14	4.8	
Total occurrences		322			290		

*$P<0.01$.
[1]Others included unidentified prey and minor prey (those with < 5 occurrences in both stomach contents and feces).

Salmon, *Oncorhynchus* spp., remains were identified in four stomachs while none were found in the fecal samples. I have examined nine harbor seal stomachs containing salmon remains and only one included a head with otoliths. It appeared that seals often fragmented large fish such as salmon while eating them, usually discarding the head. Thus, studies of feeding habits based on scat analyses (which require the presence of otoliths) probably underrepresent utilization of large fishes such as salmon. One occurrence of a cartilaginous fish was encountered (listed under others in Table 1). This was a skate, *Raja* sp., found in a stomach. It is unlikely that cartilaginous fishes would be detected in scats, as they have tiny, diffuse otoliths. (Lagler et al. 1962).

In summary, it appears that analysis of scats from harbor seals can provide accurate information on utilization of most kinds of prey. However, cephalopods, cartilaginous fishes, and large fishes such as salmon may be underrepresented. Cephalopod remains may be overrepresented in stomach contents.

Acknowledgments

This work was supported by the Alaska Department of Fish and Game and the Marine Mammal Commission and by the Bureau of Land Management through an interagency agreement with the National Oceanic and Atmospheric Administration, under which a multiyear program responding to needs of petroleum development of the Alaskan continental shelf is managed by the Outer Continental Shelf Environmental Assessment Program office. The suggestion to compare results of the two methods of analysis was made by F. Fay. Field assistance was provided by many members of the Alaska Department of Fish and Game. Thanks are due to D. Calkins, F. Fay, K. Frost, L. Lowry, D. McKnight, K. Schneider, and two anonymous reviewers for commenting on the manuscript.

Literature Cited

FISCUS, C. H., AND G. A. BAINES.
1966. Food and feeding behavior of Steller and California sea lions. J. Mammal. 47:195-200.

IMLER, R. H., AND H. R. SARBER.
1947. Harbor seals and sea lions in Alaska. U.S. Fish Wildl. Serv., Spec. Sci. Rep. 28, 23 p.

LAGLER, K. F., J. E. BARDACH, AND R. R. MILLER.
1962. Ichthyology. Wiley, N.Y., 545 p.

SPALDING, D. J.
1964. Comparative feeding habits of the fur seal, sea lion and harbor seal on the British Columbia coast. Fish. Res. Board Can., Bull. 146, 52 p.

KENNETH W. PITCHER

Alaska Department of Fish and Game
333 Raspberry Road
Anchorage, AK 99502

THE 1978 SPRING RECREATIONAL CATCH OF ATLANTIC MACKEREL, *SCOMBER SCOMBRUS*, OFF THE MIDDLE ATLANTIC REGION

Atlantic mackerel, *Scomber scombrus*, seasonally migrate through the Middle Atlantic region, usually appearing off Virginia in March with a gradual movement inshore and north until they move out of the area by mid-June. They spend the summer and early autumn north of Cape Cod, only briefly returning to the coastal waters of the Middle Atlantic in late fall, before migrating offshore and south in late December or January (Bigelow and Schroeder 1953). They are primarily available to recreational anglers along the Middle Atlantic coast during the spring migration. As Christensen et al.[1] found, the autumn catch of Atlantic mackerel in New Jersey in 1975 was <1% of the catch the following spring. Recreational catches declined from an estimated 32,000 t in 1970 (Deuel 1973) to 5,000 t in 1976 (Christensen et al. footnote 1). Although the recreational catch estimates lack measures of accuracy and reliability, the decline follows the steady decline in total stock from 2.4 million t in 1969 to 469,000 t in 1978 (Anderson 1979).

An estimate of total landings and age composition of the catch is necessary for assessment and management of the stock. This survey was initiated by personnel of the Northeast Fisheries Center (NEFC) Sandy Hook Laboratory, National Marine Fisheries Service (NMFS) in cooperation with State personnel from the Delaware Division of Fish and Wildlife, the New Jersey Division of Fish, Game and Shellfisheries, and the New York State Department of Environmental Conservation at the request of the Mid-Atlantic Fisheries Management Council. Although the request was to determine the 1978 recreational catch of Atlantic mackerel between Virginia and New York, Virginia and Maryland were not included in the survey as the Atlantic mackerel fishing season had already begun in those states.

Methods

Sampling

A list of inlets, grouped into five regions including Delaware, southern New Jersey, northern New Jersey, coastal Long Island, and Long Island Sound (Table 1) was prepared for the Middle Atlantic coastline (Figure 1). Inlets were randomly selected for weekly sampling from the list of inlets within the regions where Atlantic mackerel were known or anticipated to be present. The list indicating availability of Atlantic mackerel in an area was primarily determined by telephone conversations with marina owners and commercial sportfishing vessel operators advertising in two weekly fishing magazines, *The Fisherman*[2] and *The Long Island Fisherman*.[3] These observations were then confirmed during subsequent on-site interviews with vessel operators. In this way it was possible to concentrate sampling efforts in regions where Atlantic mackerel were available and to determine the lengths of the regional seasons.

Personnel from cooperating State agencies confined sampling to their respective states and worked primarily weekdays while NEFC personnel sampled in all regions both weekends and weekdays following the movement of Atlantic mackerel northward. Data collected before Atlan-

[1] Christensen, D. J., B. L. Freeman, and S. C. Turner. 1976. The United States recreational fishery for Atlantic mackerel. Int. Comm. NW Atl. Fish., Res. Doc. 76/XII/142, ser. no. 4038, 7 p.

[2] *The Fisherman for the New Jersey, Delmarva, and Hatteras fisherman*. NJF Publishing Corp., Sag Harbor, N.Y.

[3] *The Long Island Fisherman*. LIF Publishing Corp., Sag Harbor, N.Y.

TABLE 1.—Summary of sampling activity and dates of Atlantic mackerel availability in regions along the Middle Atlantic coast in 1978.

Region	Inlets included in region	No. of sampling days in region	Period mackerel were available	No. of days mackerel were present	
				Weekdays	Weekends
I - Delaware	Indian River	24	4 Apr.-8 May	25	10
II - Southern New Jersey	Roosevelt Cape May Hereford Townsend Corson Great Egg Absecon Beach Haven	19	8 Apr.-12 May	25	10
III - Northern New Jersey	Barnegat Manasquan Shark River Sandy Hook	22	15 Apr.-14 May	20	10
IV - South Shore Long Island	Rockaway East Rockaway Jones Fire Island Shinnecock Montauk	21	29 Apr.-28 May	20	10
V - North Shore Long Island	Greenport Mattituck Mt. Sinai Port Jefferson Stony Brook Nissequogue Northport Huntington Oyster Bay Hempstead Manhasset Bay Little Neck Bay City Island	27	5 May-8 June	25	10

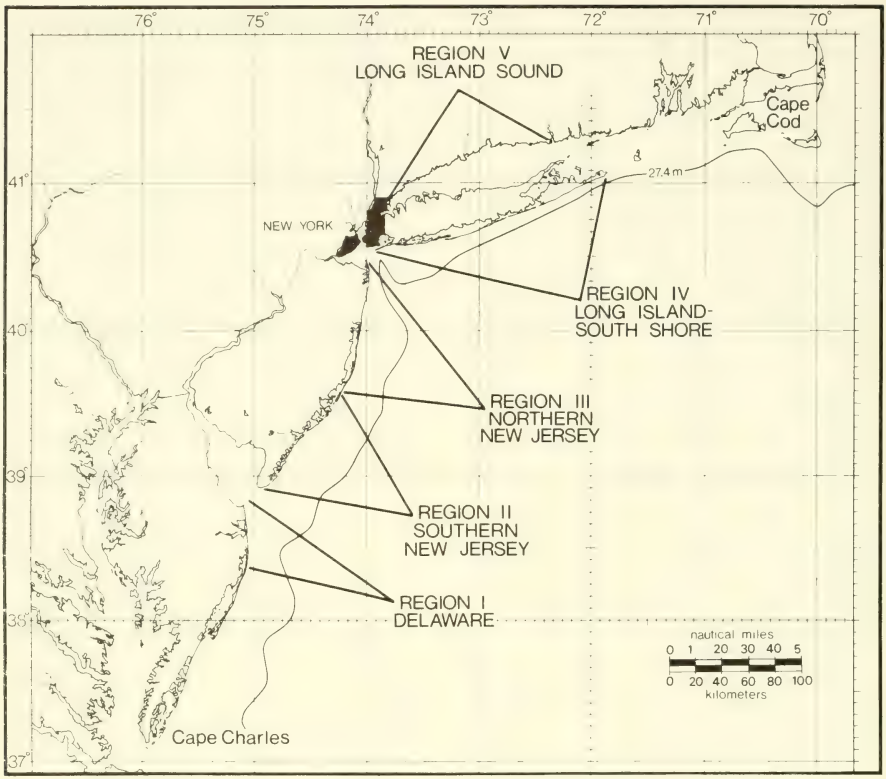


FIGURE 1.—Survey regions along the Middle Atlantic coast for recreational catch of Atlantic mackerel.

tic mackerel arrived or after they departed from a region were omitted from subsequent analysis. Boat counts were made at each inlet to determine the number of vessels sailing through the inlet, and interviews were conducted concurrently at associated marinas, docks, and launching ramps to determine the catch per vessel. There were no adequate data available on which to base proportions of interviews among different types of fishing vessels. Therefore, as many interviews as possible were made with all vessel types as they returned to port.

Inlet vessel counts were made of party, charter, and private boats. Charter boats are commercial sportfishing vessels which are usually reserved in advance by a group of fishermen for their exclusive use for a negotiated single fee. Party boats (head boats) are commercial sportfishing vessels filled on a first-come, first-served basis at an established fee per person. Party boats were subdivided into full- and half-day categories based on their daily activity schedules. Full-day party boats make a single day trip of about 7-9 h duration while half-day party boats make a morning and afternoon trip each of which is usually 4-5 h in duration. Private boats are noncommercial sportfishing vessels. The term sportfishing does not exclude the passengers or crew from selling part or all of their catch.

Estimation of Fishing Effort

NEFC and Delaware personnel counted boats either from 0500 to 1300 h or 1300 to 2000 h.

Morning counts and afternoon counts were summed to determine daily counts. New Jersey personnel counted boats passing through inlets for entire days while New York personnel concentrated efforts obtaining interviews and did not make inlet counts.

Inlets in the survey area were grouped into three size classes (small, a; medium, b; large, c) according to the maximum expected numbers of each type of vessel using the inlet. The mean and variance of the number of vessels sailing daily through inlets in each class was determined separately for weekend days and weekdays as boat traffic was frequently much greater on weekends. The mean and variance for weekend days and weekdays were combined using the following formulae (Cochran 1977):

$$\bar{s}_i = \frac{10\,\overline{we}_i + 23\,\overline{wd}_i}{10 + 23}$$

where $\bar{s}_i$ = estimated mean number of vessels sailing daily in inlet class i, where $i = a, b, c$

$\overline{we}_i$ = estimated mean number of vessels sailing daily on weekend days in inlet class i

$\overline{wd}_i$ = estimated mean number of vessels sailing daily on weekdays in inlet class i

10 = mean number of weekend days in season

23 = mean number of weekdays in season

and the estimated variance of $\bar{s}_i$ is:

$$\hat{v}(\bar{s}_i) = \left(\frac{10}{10+23}\right)^2 \hat{v}(\overline{we}_i) + \left(\frac{10}{10+23}\right)^2 \hat{v}(\overline{wd}_i)$$

where $\hat{v}(\bar{s}_i)$ = estimated variance of mean number of vessels sailing daily in inlet class i

$\hat{v}(\overline{we}_i)$ = estimated variance of mean number of vessels sailing daily on weekend days in inlet class i

$\hat{v}(\overline{wd}_i)$ = estimated variance of mean number of vessels sailing daily on weekdays in inlet class i

10 and 23 = constants as above.

The mean, variance, and confidence interval of the number of vessels of each type sailing daily in all inlet classes was determined by combining the means and variances according to the following formulae (Cochran 1977):

$$\bar{s} = \frac{N_a \bar{s}_a + N_b \bar{s}_b + N_c \bar{s}_c}{N_a + N_b + N_c}$$

where $\bar{s}$ = mean number of vessels sailing daily through all inlets where the vessel type occurs

N_a, N_b, N_c = number of inlets in inlet classes a, b, and c

$\bar{s}_a, \bar{s}_b, \bar{s}_c$ = mean number of vessels sailing daily through inlet classes a, b, and c

$$\hat{v}(\bar{s}) = \left(\frac{N_a}{N_a + N_b + N_c}\right)^2 \hat{v}(\bar{s}_a) + \left(\frac{N_a}{N_a + N_b + N_c}\right)^2 \hat{v}(\bar{s}_b) + \left(\frac{N_a}{N_a + N_b + N_c}\right)^2 \hat{v}(\bar{s}_c)$$

where $\hat{v}(\bar{s})$ = estimated variance of $\bar{s}$

$\hat{v}(\bar{s}_a), \hat{v}(\bar{s}_b), \hat{v}(\bar{s}_c)$ = estimated variance of $\bar{s}_a$, $\bar{s}_b$, and $\bar{s}_c$

$$CI = \bar{s} \pm 1.96 \sqrt{\hat{v}(\bar{s})}$$

where CI = 95% confidence interval about $\bar{s}$.

Estimation of Catch Rates

Interviews were made at dock sites, marinas, and launching ramps to determine vessel catches. Vessel catches were determined rather than individual angler catches since most private boat and charter boat anglers share their total catches. In addition, while some party boat anglers may fish as individuals, it is common practice for family or social groups to share a common fish container making it impossible to determine the exact catch per angler. During interviews the type of vessel, fishing location, interview site location, number of Atlantic mackerel caught, and fork lengths (FL) of Atlantic mackerel were recorded.

Inspection of the distribution of catch per vessel indicated a lognormal distribution. Therefore, the catch numbers were first converted to natural logs and then the means and

variances were calculated for each vessel type over the entire survey area. The log mean and log variance for each vessel type was transformed, and the 95% confidence interval about the retransformed mean was calculated according to the following formulae (Aitchison and Brown 1957):

$$c = \exp\left(\bar{L} + {}^{1}\!/_{2}\left(\frac{n-1}{n}\right)\hat{v}(\bar{L})\right)$$

where $\bar{c}$ = mean catch per vessel
$\bar{L}$ = mean natural log of catch per vessel
$\hat{v}(\bar{L})$ = estimated variance of natural logs to catch per vessel
n = number of vessels interviewed

The variance of $\bar{c}$, $\hat{v}(\bar{c})$, is approximated by:

$$\frac{c}{n}^{2}\left\{\hat{v}(\bar{L}) + {}^{1}\!/_{2}(\hat{v}(\bar{L}))^{2}\right\}$$

and

$$\bar{c} \pm 1.96\sqrt{\hat{v}(\bar{c})}$$

is a 95% confidence interval about $\bar{c}$.

Estimated Total Catches

The mean catch per inlet per day, its variance assuming $\bar{s}$ and $\bar{c}$ were independent, and 95% confidence intervals were calculated for each vessel type using the following formulae:

$$\overline{sc} = \bar{s} \times \bar{c}$$

where $\overline{sc}$ = mean catch per inlet per day
$\bar{s}$ = mean trips per inlet per day
$\bar{c}$ = mean catch per vessel

$$\hat{v}(\overline{sc}) = (\bar{s})^2\,\hat{v}(\bar{c}) + (\bar{c})^2\,\hat{v}(\bar{s}) + \hat{v}(\bar{c})\,\hat{v}(\bar{s})$$

where $\hat{v}(\overline{sc})$ = estimated variance of catch per inlet per day
$\hat{v}(\bar{s})$ = estimated variance of trips per inlet per day
$\hat{v}(\bar{c})$ = estimated variance of catch per vessel

$$\text{CI} = \overline{sc} \pm 1.96\sqrt{\hat{v}(\overline{sc})}$$

where CI = 95% confidence interval about $\overline{sc}$

The total estimated catch (TSC) per vessel type and the 95% confidence interval about the estimate were calculated as follows:

$$TSC = \left[\overline{sc} \pm 1.96\sqrt{\hat{v}(\overline{sc})}\right] \times 33NI$$

where TSC = total estimated catch
NI = number of inlets where vessel type occurred
33 = number of days in fishing season

The total estimated catch and confidence interval for the total survey area and all vessel types were determined by summing the estimated catches and extracting the square root of the sum of the squares of the variances of all four vessel types.

Lengths, Weights, and Age Composition of Catches

A total of 2,778 Atlantic mackerel were measured to the nearest centimeter fork length to determine the length frequencies of the catch. Each length was converted to a weight using the formula $\log_{10}$ weight $= -5.2314 + 3.0796 \log_{10}$ length (Wilk et al. 1978), and a mean weight was calculated for all vessel types. The mean weight was multiplied by the total estimated number caught to determine the total weight of the catch.

For age composition analysis, Atlantic mackerel were obtained in April from recreational and commercial fishermen fishing primarily along the New Jersey coast and transported to the NEFC Sandy Hook Laboratory where they were measured to the nearest centimeter fork length and sexed. The heads were removed, frozen, and sent to the NEFC Woods Hole Laboratory, NMFS, for otolith removal and aging. Aging was accomplished by placing intact otoliths in black trays, imbedding them in clear epoxy resin, and counting annular rings using reflected light at 25-75× magnification under a binocular microscope. The number of fish from the length-frequency sample of 2,778 measured at each centimeter length was multiplied by the percentage age composition at that length increment to determine the number of fish caught in each age-group at each centimeter increment. The numbers at each age were summed from all length increments and divided by the total number of fish measured to determine the percentage composition of each age in the recreational catch. The percentage composition at each age was multiplied by the total estimated Middle

Atlantic catch to determine the estimated total recreational catch by age-class in the Middle Atlantic region.

Results and Discussion

Privately owned boats were by far the most numerous type observed using inlets during the survey (Table 2). The mean catch per vessel was lowest for private boats, intermediate for half-day party and charter boats, and highest for full-day party boats (Table 2). Full-day party boats anglers caught the most Atlantic mackerel during the season followed in decreasing order by anglers aboard private boats, half-day party boats, and charter boats (Table 3). The total estimated number of mackerel caught in the survey area was 6,792,000±2,415,000.

The mean fork length of all Atlantic mackerel measured during the survey was 37.9 cm and the calculated mean weight was 0.515 kg/fish. The total estimated weight caught was 3,498 ±1,244 t.

The survey was initiated after Atlantic mackerel had already progressed north into waters off Delaware and southern New Jersey. Therefore, it was too late to survey catches in the southern portion of the Middle Atlantic region. Maryland has a single inlet at Ocean City with a few party boats, a modest number of charter boats, and facilities for private boats. Virginia has several locations such as Chincoteague, Wachapreague, and Quinby along the coast of the Delmarva Peninsula where some charter and private boats have ocean access, and two inlets (Rudee and Lynnhaven) near the mouth of Chesapeake Bay where a few party boats and a number of charter and private boats have ocean access to fish for Atlantic mackerel. The catch made from Delaware's only two coastal inlets was about 8% of the Delaware and New Jersey total. Assuming similar levels of effort and catch at the six inlets in Maryland and Virginia, the Maryland and Virginia catches were approximately 25% of the New Jersey and Delaware total. The combined catch within the Delaware and New Jersey regions was about 34% of the catch (3,498 t) of the three-State area surveyed or 1,189 t. Thus, the total estimated catch for Virginia-New Jersey was 125% of 1,189 t or 1,486 t.

The number of party and charter boats in New York was found to be approximately equal to the combined fleets in Connecticut through Maine (Fraser et al. 1977). Assuming similar levels of Atlantic mackerel caught by commercial sportfishing vessels and private vessels in Connecticut-Maine, New York catches accounted for 50% of the North Atlantic regional catch (New York-Maine) (Deuel 1973). The New York portion of the Delaware, New Jersey-New York catch was about 66% or 2,309 t of the 3,498 t total catch. Therefore, the Connecticut-Maine catch was assumed to also be 2,309 t, giving a New York-Maine total of 4,617 t. The total recreational catch of Atlantic mackerel taken by boat in the Virginia-Maine area was estimated to be 6,103 t of which 3,795 t was caught in the New York-Virginia area.

A total of 278 Atlantic mackerel were aged from samples collected during the survey. The ages were found to range from 2 to >11 yr with considerable overlap of age-classes at >36 cm FL (Table 4). The range of all fish measured during the survey was 27-44 cm FL (Table 5) and the mean was 37.9 cm. It is apparent from the estimated total catch by ages (Table 5) that fish caught by recreationsl anglers came mainly from the older age-groups. The remnants of the

TABLE 2.—Average number of trips and catches of Atlantic mackerel by sportfishing vessels during the Middle Atlantic coast survey, 1978.

Vessel type	Mean trips per inlet per day	95% confidence interval	Mean catch per vessel trip	95% confidence interval
Party boats:				
Full-day	3.87	±1.37	1,425	±542
Half-day	3.92	±1.75	352	±154
Charter boats	2.82	±1.11	346	±106
Private boats	56.41	±7.25	45	±8

TABLE 3.—Summary of catches of Atlantic mackerel made by sportfishing vessels encountered during the 1978 survey of the Middle Atlantic coast.

Vessel type	Mean catch per inlet per day	95% confidence interval	Number of inlets where vessel type occurred	Total estimated catch	95% confidence interval
Party boats:					
Full-day	5,515	±3,673	19	3,458,000	±2,303,000
Half-day	1,380	±604	8	364,000	±159,000
Charter boats	976	±483	9	290,000	±143,000
Private boats	2,538	±658	32	2,680,000	±695,000
Total				6,792,000	±2,415,000

TABLE 4.—Percentage age at length of Atlantic mackerel aged from samples collected during the 1978 spring sportfishing season along the Middle Atlantic coast.

Fork length (cm)	No.	Age (years)										
		2	3	4	5	6	7	8	9	10	11	>11
27	1	100.0										
28	1	100.0										
29	1	100.0										
30	1		100.0									
31	1			100.0								
32	11		27.3	72.7								
33	38		5.3	73.7	21.0							
34	57		12.3	63.2	19.3	5.3						
35	41		7.3	41.5	43.9	7.3						
36	29		6.9	13.8	6.9	37.8	13.9		20.7			
37	42		4.8	11.9	7.1	21.4	11.9		23.8	2.4	14.3	2.4
38	29				3.4	13.8	24.1	3.4	20.7	3.4	31.0	
39	21							9.5	38.1	4.8	33.0	14.3
40	4								25.1		50.0	25.0
41	1										100.0	
Total	278											

TABLE 5.—Numbers, percentage age composition, mean length at age of recreationally caught Atlantic mackerel, and estimated recreational catch in metric tons from New York through Virginia during 1978.

Fork length (cm)	Age (years)											Total
	2	3	4	5	6	7	8	9	10	11	>11	
27	1											1
28	2											2
30		2										2
32		1	3									4
33		1	17	5								23
34		8	42	13	4							67
35		9	51	55	9							124
36		18	35	18	96	35		53				255
37		28	69	41	124	69		138	14	83	14	580
38				25	100	176	25	151	25	226		728
39							55	221	28	194	83	581
40								72		143	72	287
41										94		94
42											24	24
43											5	5
44											1	1
Total	3	67	217	157	333	280	80	635	67	740	199	2,778
Percentage of total	0.1	2.4	7.8	5.7	12.0	10.1	2.9	22.9	2.4	26.6	7.2	100.1
Mean length at age, cm	27.7	35.8	35.4	36.0	36.9	37.5	38.7	38.7	38.2	38.9	—	—
Estimated total catch (t) by age	4	92	296	214	455	383	109	867	92	1,011	272	3,795

large 1967 and 1969 year classes (Anderson 1979) which were 11 and 9 yr old in 1978 still contributed nearly 50% of the recreational catch. The percentage age composition of the total stock in 1978 was estimated to be 23.1, 17.0, 22.7, 25.2, 7.0, 1.4, 1.2, 0.8, 0.8, 0.5, 0.4, and 0.1 for ages 1 through 11 and >11 (Anderson 1979). Comparisons of the two age composition estimates indicates all age-groups older than 5 compose 5.1% of the stock and 84.1% of the recreational catch. The mean fork length of age-class 3 through 5 fish was only 2.2 cm less than the mean fork length of all fish measured during the recreational survey. Therefore, it does not seem probable that the hook-and-line fishery is size selective between age-classes >2 yr old. The stock assessment (Anderson 1979) was based partially on NMFS research vessel trawl surveys which did not include sampling inside the 27.4 m (15 fathom) contour. As most recreational fishing is done inshore of the 27.4 m contour, it is possible that older Atlantic mackerel concentrate inshore. This would result in a delay in recruitment into the recreational fishery until age 6 or greater.

Acknowledgments

We wish to express our appreciation to the following personnel who assisted in the collection of field data: Pernell Lewis, Robert Matus, William Rogers, Russell Terranova, and Paul Yuschak, NMFS; Ronal W. Smith, Delaware Division of Fish and Wildlife; Paul G. Scarlett, Barry Preim,

Raymond Townsend, and Joseph D. Vaughn, New Jersey Division of Fish, Game, and Shellfish; Donald Zacchae, Egbert Howell, and Al Kilthan, New York State Department of Environmental Conservation.

We also wish to thank Michael Pennington for suggesting use of the lognormal transformation to determine mean vessel catches, and Judy Pentilla and Louise Dery for determining ages of the Atlantic mackerel.

Literature Cited

AITCHISON, J., AND A. C. BROWN.
1957. The log normal distribution with special reference to its uses in economics. Camb. Univ. Press, Camb., 176 p.

ANDERSON, E. D.
1979. Assessment of the Northwest Atlantic mackerel, *Scomber scrombrus*, stock. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-732, 13 p.

BIGELOW, H. B., AND W. C. SCHROEDER.
1953. Fishes of the Gulf of Maine. U.S. Fish. Wild. Serv., Fish. Bull. 74, 577 p.

COCHRAN, W. G.
1977. Sampling techniques. 3d ed. Wiley, N.Y., 428 p.

DEUEL, D. G.
1973. The 1970 salt-water angling survey. U.S. Dep. Commer., Cur. Fish. Stat. 6200, 54 p.

FRASER, M. B., J. A. HENDERSON, AND J. F. MCNAUS.
1977. Survey of commercial sportfishing boats in the coastal United States. Oreg. State Univ., Sea Grant Coll. Program, Publ. ORESU-T-77-009, 28 p.

WILK, S. J., W. W. MORSE, AND D. E. RALPH.
1978. Length-weight relationships of fish collected in the New York Bight. Bull. N.J. Acad. Sci. 23(2):58-64.

DARRYL J. CHRISTENSEN
WALTER J. CLIFFORD

Northeast Fisheries Center Sandy Hook Laboratory
National Marine Fisheries Service, NOAA
Highlands, NJ 07732

SIZE AND POSSIBLE ORIGIN OF SAILFISH, *ISTIOPHORUS PLATYPTERUS*, FROM THE EASTERN ATLANTIC OCEAN[1]

Although Morrow and Harbo (1969) considered the sailfish, *Istiophorus platypterus*, to be a single worldwide species, other workers believe that the Atlantic and Pacific forms are separate species (Nakamura et al. 1968; Nakamura 1974). It has long been recognized that Indo-Pacific specimens, particularly those found along the coasts of Panama and Mexico, attain a much greater size than do their Atlantic counterparts. In addition, the form of the spinous dorsal fin differs in fish from the two ocean areas. The International Game Fish Association (IGFA), which keeps detailed and precise records of the largest fish caught in various sportfishing categories, maintains separate records for Indo-Pacific and Atlantic sailfish. At present, the largest sailfish caught by sportfishing gear in the Pacific weighed 100.2 kg, and of the 14 different line test categories recorded by IGFA, only two record Pacific sailfish weighed <70 kg. In contrast, the largest Atlantic specimen weighed 58.1 kg and over half of the record catches were <50 kg (International Game Fish Association 1980). Morrow and Harbo (1969) stated that it was probable that improved nutrition, better conditions for growth, or some other favorable environmental condition was responsible for the attainment of the greater size in Indo-Pacific sailfish.

Size data for Atlantic sailfish caught by the Japanese longline fishery in various areas of the Atlantic have recently become available in the annual publications of the International Commission for the Conservation of Atlantic Tunas.[2] These data show that unusually large sailfish also occur in the Atlantic, specifically in the eastern Atlantic off the coast of Africa between lat. 0° and 20° S (Figure 1; Areas F, G). Size frequencies from the region indicate fish of substantially greater size than from any of the other areas in the Atlantic where size data from sailfish caught by the longline fishery were available (Figure 2). I calculated the weights of eastern Atlantic specimens using length-weight relationships developed by various authors (Table 1). The results (Table 2) show increasing variation in calculated weights as fish length increases; however, regardless of which

[1]Southeast Fisheries Center Contribution No. 80-05M.

[2]International Commission for the Conservation of Atlantic Tunas, Madrid, Data Records Vol. 10, p. 303-304 and Vol. 11, p. 267-270.

TABLE 1.—Coefficients of the length-weight relationship for western Atlantic sailfish (Lenarz and Nakamura 1974; Jolley 1974) and eastern Pacific sailfish (Kume and Joseph 1969; Wares and Sakagawa 1974). All lengths are from posterior rim of orbit to fork except Jolley, which is from orbit to origin of caudal keels. Calculated weights will be in kilograms except for Lenarz and Nakamura which will be in pounds.

Author	No. of specimens	Size range	log a	b
Lenarz and Nakamura (1974)	244	15.8-62.5 in	−3.895	3.158
Jolley (1974) Male	182	76-156 cm	−5.784	3.342
Female	230	47-164 cm	−4.941	2.950
Kume and Joseph (1969)	28	134-205 cm	−3.936	2.416
Wares and Sakagawa (1974)	802	115-222 cm	−4.360	2.628

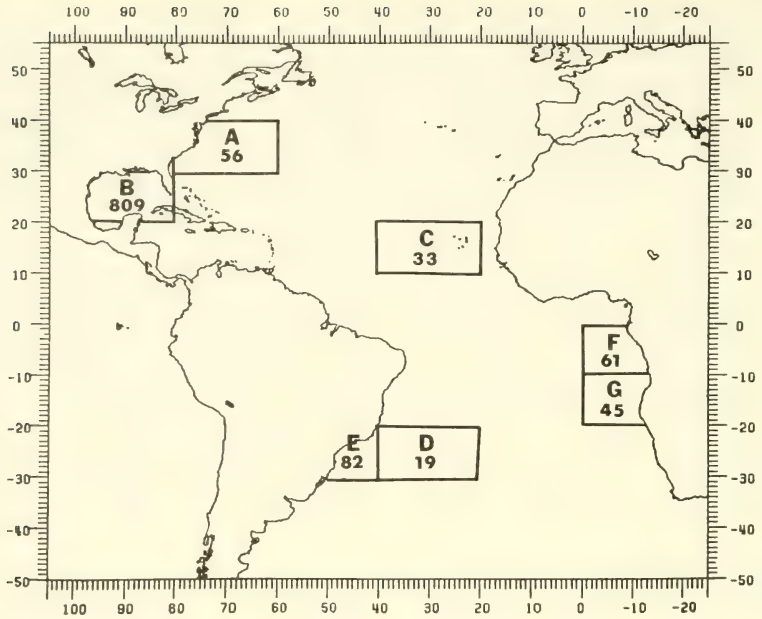


FIGURE 1.—Areas and number of sailfish sampled from the Japanese longline fishery in the Atlantic, 1975-76. Data are from Data Records 10, 11, International Commission for the Conservation of Atlantic Tunas (see text footnote 2).

TABLE 2.—Estimated weights of sailfish caught by longline gear in the eastern Atlantic (Figure 1; Areas F, G) using length-weight relationships from various authors.

Author	Smallest[1] (148.5 cm)	Average (174.8 cm)	Largest (223.5 cm)
	estimated weight, kg		
Lenarz and Nakamura (1974)[2]	21.9	36.7	79.9
Jolley (1974)[3] Male	22.9	39.8	91.0
Female	23.2	37.7	78.3
Kume and Joseph (1969)	20.5	30.3	54.9
Wares and Sakagawa (1974)	22.2	34.2	65.2
Average length in other five areas 140.7 cm			
Average weight in other five areas 18.6 kg (Lenarz and Nakamura formula)			

[1]There was one specimen measuring 116-120 cm fork length but was excluded from this demonstration.

[2]Lenarz and Nakamura conducted their calculations in inches and pounds. I converted results using their formula into kilograms for this demonstration.

[3]Although Jolley's formula indicates that males in the eastern Atlantic attain a greater weight at a given length than females, available evidence indicates that this is not true for western Atlantic sailfish. Only a few females in Jolley's sample were as large as the average-sized eastern Atlantic specimen and the indication that males attain a greater weight is probably a result of extrapolation of Jolley's formula beyond the limits of his data.

formula one uses, it is clear that the eastern Atlantic specimens are unusually large fish (it should be noted that estimated weights in Table 2 may be significantly affected by an unknown logarithmic bias inherent in the length-weight parameters). Using Lenarz and Nakamura's (1974) formula, for example, the average weight of sailfish sampled in the eastern Atlantic was only 21.4 kg less than the current all-tackle world record for Atlantic sailfish, and the largest specimens were 21.8 kg larger than the all-tackle record. There is currently little sport fishing in the eastern Atlantic; however, between 1971 and 1975 seven world records were established for Atlantic sailfish off the coast of Angola, including the current all-tackle record of 58.1 kg.

There are striking similarities between the distribution of sailfish in the Pacific and Atlantic Oceans. In both oceans, sailfish appear to be most abundant on the western side and have a greater north-south range than on the eastern side (Koto et al. 1959; Kume and Joseph 1969; Ueyanagi et al. 1970). The largest specimens are apparently located on the eastern side of their respective oceans and in a fairly localized area. Size data on sailfish from the eastern Pacific presented by Kume and Joseph (1969) and Wares and Sakagawa (1974)

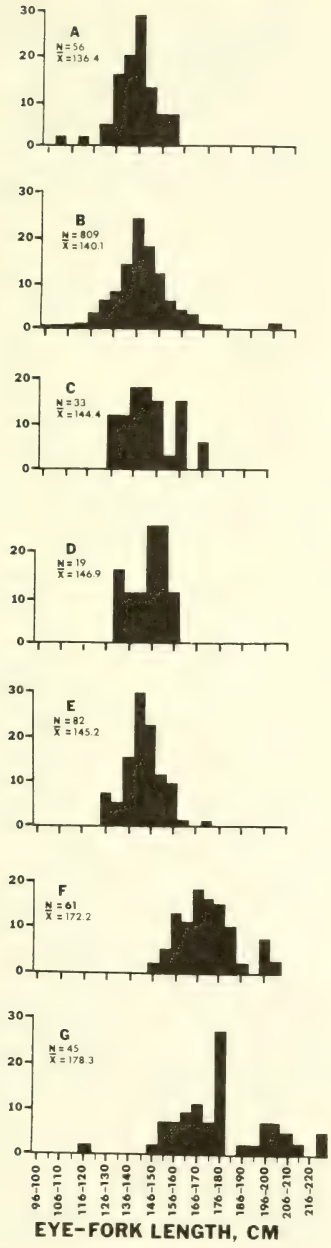


FIGURE 2.—Length frequencies of sailfish captured by the Japanese longline fishery in the Atlantic, 1975-76. Letters indicate areas from Figure 1.

agree quite well with similar data on eastern Atlantic specimens sampled off the coast of Africa, both in range and average length. Additionally, size frequencies of sailfish from the East China Sea (Koto et al. 1959) are quite similar to size data for western Atlantic sailfish given by Jolley (1977). In both the eastern Pacific and eastern Atlantic, sailfish occur in an area where a substantial surface fishery for yellowfin and skipjack tunas takes place. Fox[3], in his analysis of the temporal and spatial relationships among tunas and billfishes in the Atlantic, showed a strong correlation between the occurrence of sailfish and yellowfin tuna in the Atlantic and a strong relationship between the occurrence of the two species and surface water temperatures.

There are also similarities in the environment on the eastern sides of the Atlantic and Pacific Oceans where the largest specimens of sailfish occur. Both areas have relatively shallow thermoclines. Thermal domes occur in both the eastern Atlantic (Mazeika 1967) and the eastern Pacific (Wyrtki 1964) and probably influence the seasonal distribution of at least some oceanic fishes (Beardsley 1969).

It seems possible, therefore, that environmental conditions in both the eastern Pacific and eastern Atlantic favor rapid growth and the attainment of a large size in sailfish.

There is also the possibility that the group of large sailfish off Africa are immigrants from the Indian Ocean around the tip of South Africa. Other large oceanic fishes, such as the albacore, *Thunnus alalunga*, and the black marlin, *Makaira indica*, are suspected to have entered the Atlantic by this route (Koto 1969; Wise and Davis 1973), and Penrith and Cram (1974) reported that six species of billfishes have been recorded in waters west and south of the Cape of Good Hope. The sailfish, however, was not included in this group. Even though Penrith and Cram did not find sailfish in their samples, the presence of other istiophorids suggests that sailfish probably are present at times in this area.

The sizes of sailfish from the eastern Atlantic and the western Indian Ocean are similar. Merrett

[3]Fox, W. W., Jr. 1971. Temporal-spatial relationships among tunas and billfishes based on the Japanese longline fishery in the Atlantic Ocean, 1956-1965. Univ. Miami Sea Grant Tech. Bull. 12, 78 p.

(1971) examined 77 sailfish caught on longlines off East Africa and found that the majority were between 160 and 185 cm body length (center of orbit to tip of shortest caudal ray), which is consistent with the modes found for sailfish off Africa (Figure 2).

It seems possible, then, that when oceanographic conditions are favorable, sailfish move from the western Indian Ocean to the eastern Atlantic around the tip of South Africa. Based on the size samples available from the longline fishery in other areas of the Atlantic and size frequencies of sailfish caught in the sport fishery in the western Atlantic (de Sylva 1957; Jolley 1977), these fish apparently remain in a fairly restricted area off the coast of West Africa.

Acknowledgments

I thank John Jolley, C. Richard Robins, Donald P. de Sylva, and Francis Williams for reviewing the manuscript.

Literature Cited

BEARDSLEY, G. L., JR.
1969. Distribution and apparent relative abundance of yellowfin tuna (*Thunnus albacares*) in the eastern tropical Atlantic in relation to oceanographic features. Bull. Mar. Sci. 19:48-56.

DE SYLVA, D. P.
1957. Studies on the age and growth of the Atlantic sailfish, *Istiophorus americanus* (Cuvier), using length-frequency curves. Bull. Mar. Sci. Gulf Caribb. 7:1-20.

INTERNATIONAL GAME FISH ASSOCIATION.
1980. World record game fishes. Int. Game Fish Assoc., Ft. Lauderdale, Fla., 287 p.

JOLLEY, J. W., JR.
1974. On the biology of Florida east coast Atlantic sailfish (*Istiophorus platypterus*). *In* R. S. Shomura and F. Williams (editors), Proceedings of the International Billfish Symposium, Kailua-Kona, Hawaii, 9-12 August 1972, Part 2. Review and contributed papers, p. 81-88. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-675.
1977. The biology and fishery of Atlantic sailfish, *Istiophorus platypterus*, from southeast Florida. Fla. Mar. Res. Publ. 28, 31 p.

KOTO, T.
1969. Studies on the albacore—XIV. Distribution and movement of the albacore in the Indian and the Atlantic Oceans based on the catch statistics of Japanese tuna long-line fishery. Bull. Far Seas Fish. Res. Lab. (Shimizu) 1:115-129.

KOTO, T., I. FURUKAWA, AND K. KODAMA.
1959. Studies on the tuna longline fishery in the East China Sea - III. Ecological studies on the sailfish. [In Jpn., Engl. abstr.] Rep. Nankai Reg. Fish. Res. Lab. 10:88-106.

KUME, S., AND J. JOSEPH.
1969. Size composition and sexual maturity of billfish caught by the Japanese longline fishery in the Pacific Ocean east of 130°W. Bull. Far Seas Fish. Res. Lab. (Shimizu) 2:115-162.

LENARZ, W. H., AND E. L. NAKAMURA.
1974. Analysis of length and weight data on three species of billfish from the western Atlantic Ocean. *In* R. S. Shomura and F. Williams (editors), Proceedings of the International Billfish Symposium, Kailua-Kona, Hawaii, 9-12 August 1972, Part 2. Review and contributed papers, p. 121-125. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-675.

MAZEIKA, P. A.
1967. Thermal domes in the eastern tropical Atlantic Ocean. Limnol. Oceanogr. 12:537-539.

MERRETT, N. R.
1971. Aspects of the biology of billfish (Istiophoridae) from the equatorial western Indian Ocean. J. Zool. (Lond.) 163:351-395.

MORROW, J. E., AND S. J. HARBO.
1969. A revision of the sailfish genus *Istiophorus*. Copeia, 1969:34-44.

NAKAMURA, I.
1974. Some aspects of the systematics and distribution of billfishes. *In* R. S. Shomura and F. Williams (editors), Proceedings of the International Billfish Symposium, Kailua-Kona, Hawaii, 9-12 August 1972, Part 2. Review and contributed papers, p. 45-53. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-675.

NAKAMURA, I., T. IWAI, AND K. MATSUBARA.
1968. A review of the sailfish, spearfish, marlin and swordfish of the world. [In Jpn.] Kyoto Univ., Misaki Mar. Biol. Inst., Spec. Rep. 4, 95 p.

PENRITH, M. J., AND D. L. CRAM.
1974. The Cape of Good Hope: a hidden barrier to billfishes. *In* R. S. Shomura and F. Williams (editors), Proceedings of the International Billfish Symposium, Kailua-Kona, Hawaii, 9-12 August 1972, Part 2. Review and contributed papers, p. 175-187. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-675.

UEYANAGI, S., S. KIKAWA, M. UTO, AND Y. NISHIKAWA.
1970. Distribution, spawning, and relative abundance of billfishes in the Atlantic Ocean. [In Jpn., Engl. synop.] Bull. Far Seas Fish. Res. Lab. (Shimizu) 3:15-55.

WARES, P. G., AND G. T. SAKAGAWA.
1974. Some morphometrics of billfishes from the eastern Pacific Ocean. *In* R. S. Shomura and F. Williams (editors), Proceedings of the International Billfish Symposium, Kailua-Kona, Hawaii, 9-12 August 1972, Part 2. Review and contributed papers, p. 107-120. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-675.

WISE, J. P., AND C. W. DAVIS.
1973. Seasonal distribution of tunas and billfishes in the Atlantic. U.S. Dep. Commer., NOAA Tech. Rep, NMFS SSRF-662, 24 p.

WYRTKI, K.
1964. Upwelling in the Costa Rica Dome. U.S. Fish Wildl. Serv. Fish Bull. 63:355-372.

GRANT L. BEARDSLEY

Southeast Fisheries Center Miami Laboratory
National Marine Fisheries Service, NOAA
75 Virginia Beach Drive
Miami, FL 33149

AMMONIA CONCENTRATIONS IN PINK SALMON, *ONCORHYNCHUS GORBUSCHA*, REDDS OF SASHIN CREEK, SOUTHEASTERN ALASKA

Although the toxic effects of ammonia have been observed in developing salmonids in hatcheries, few measurements of ammonia are available from the natural environment. In the fall of 1969, ammonia levels in the surface waters of Sashin Creek, southern Baranof Island, southeastern Alaska, were measured during and after the run of pink salmon, *Oncorhynchus gorbuscha*. Ammonia levels increased significantly after the run. This increase was attributed to the large number of decaying carcasses of spawned-out adult salmon (Brickell and Goering 1972). Low levels of ammoniacal nitrogen have been found in samples of intragravel waters of Sashin Creek taken in August, just before most fish spawned (McNeil et al. 1964). Ammonia concentrations have not been measured in intragravel water taken directly from salmon redds with known densities of eggs or alevins.

The transition period just before and during emergence of alevins from the gravel is critical for survival of young salmon. The young salmon have a higher rate of metabolism than eggs and early alevins (Bailey et al. 1980) and are undergoing physiological changes to enable them to actively swim and feed rather than reside quietly in the gravel. Salmonid alevins nearing the end of yolk absorption excrete ammonia at a higher rate than eggs or early alevins (Rice and Stokes 1975; Bailey et al. 1980) and are more sensitive to ammonia than earlier stages (Penaz 1965; Rice and Stokes 1975; Rice and Bailey 1980). At the same time (winter and spring), freezing weather usually causes surface and intragravel water flows to be low and thus reduces the removal rate of excreted ammonia. In 1972 we measured ammonia in samples of intragravel water taken from random sites in Sashin Creek, including pink salmon redds, and measured densities of live and dead alevins at each sample site. In this paper we report the concentrations of total ammonia (un-ionized and ionized) found in stream and intragravel water and discuss the effect of ammonia concentrations on developing alevins.

Methods

In late March we sampled 60 random intragravel sites and 4 typical surface sites. Water flow in Sashin Creek was low, which was normal for late March—the rainy season had not begun and the winter snow was not melting. The water temperature was 1.6° C and pH was 6.7. Samples of intragravel water were taken from standpipes (McNeil 1962; McNeil et al. 1964). Water samples were frozen in glass bottles within 2 h of sampling and kept frozen until analyzed within 3 d.

We determined concentrations of total ammonia ($NH_3 + NH_4^+$) using an automated method that quantitates the intensity of blue indophenol after reaction of ammonia with alkaline phenol hypochlorite (U.S. Environmental Protection Agency [EPA] 1974). The EPA method was modified by stabilizing the heat source during the reaction to increase sensitivity to a detection limit of 0.004 ppm ammonia. Analyses were made on freshly thawed water samples. Some samples and standards of known concentration were measured, frozen, and thawed a second time, and again measured. The ammonia levels did not change, indicating that our preserving technique was adequate. The slightly acid water of Sashin Creek aided in the retention of ammonia.

The density of eggs and alevins was measured at each site within 2 h of sampling for ammonia. We sampled an area of 0.1 m^2, centered on the standpipe site, with a hydraulic egg-pump (McNeil 1964), and counted dead eggs, live eggs, and alevins.

Concentrations of Ammonia in Intragravel Water and its Implications

Concentrations of ammonia and densities of eggs and alevins varied widely. Total ammonia in intragravel waters ranged from 0.008 to 0.240 ppm, and density of live eggs and alevins ranged from 0 to 352/0.1 m^2 (average 21.2) (Table 1). The densities of pink salmon eggs and alevins found in Sashin Creek were typical of many streams in southeastern Alaska[1].

The concentrations of ammonia were not correlated with location in the stream ($r = -0.18$, $P > 0.05$ for ammonia concentrations measured in

[1]The average densities of pink salmon alevins for 96 pink salmon streams of southeastern Alaska, 1966-1974, varied from <1 to 30 alevins/0.1 m^2 (Kingsbury, A., P. Larson, and G. Downey. 1975. Forecast of the 1975 pink salmon returns to southeastern Alaska. Alaska Dep. Fish Game, Inform. Leafl. 168, 33 p., on file at Northwest and Alaska Fish. Cent., Auke Bay Lab., Natl. Mar. Fish. Serv., NOAA, P.O. Box 155, Auke Bay, AK 99821).

TABLE 1.—Density of salmon eggs and alevins, and concentration of ammonia in intragravel waters of Sashin Creek, southeastern Alaska. Pink salmon eggs or alevins predominated, although a few coho salmon, *Oncorhynchus kisutch*, eggs, <10%, were occasionally present at the sample sites and are included in the totals. Four surface samples were also measured, ranging from 0.005 to 0.019 ppm total ammonia (average 0.013 ppm).

Sample site number	Number of eggs and alevins/0.1 m²			Total ammonia (ppm)
	Dead	Live	Total	
Sites with highest numbers of eggs and alevins				
8	12	352	364	0.018
189	138	107	245	0.010
190	232	0	232	0.010
10	6	213	219	0.015
97	193	11	204	0.035
Sites with highest concentrations of ammonia ($NH_3 + NH_4^+$)				
95	0	2	2	0.240
92	10	0	10	0.240
100	4	0	4	0.115
87	3	0	3	0.065
105	41	9	50	0.065
Combined values for all 60 sites				
Mean ±95% confidence interval	23.6±12.3	21.2±15.0		0.035±0.012
Range	0-232	0-352		0.005-0.240

upstream versus downstream locations) nor with the density of eggs and alevins ($r = -0.17, P > 0.10$) (Table 1). None of the five sample sites with the highest ammonia concentrations was among the five sites with the highest densities of eggs and alevins.

The lack of correlation of ammonia concentrations with alevin densities may be due to the variability of intragravel water flow. Intragravel water flow varies considerably from site to site in all streams and is affected by surface water velocity, volume of water flow, stream gradient, gravel size, and obstructions such as trees or ice (Vaux 1968). Intragravel flow may differ in adjacent redds (cross-stream or upstream-downstream). Brickell and Goering (1972) found that ammonia concentrations in surface waters of Sashin Creek during the fall spawning were generally greater at the downstream sites than at the upstream sites. In contrast, we found no relation between concentrations of ammonia sampled in the spring from intragravel waters at upstream and downstream sites at Sashin Creek. Furthermore, the concentrations of ammonia in surface water in our study were much lower and more uniform than the concentrations in the intragravel water. We conclude that measurements of ammonia in surface water are poor estimates of ammonia concentrations of intragravel water.

Twice each year, in early spring and in fall, ammonia concentrations in salmon streams can be expected to reach levels potentially harmful to salmon eggs and alevins. In the fall, a large mass of decaying salmon carcasses may litter the stream. Brickell and Goering (1972) measured ammoniacal nitrogen in surface waters of Sashin Creek during and after a heavy run of salmon and found concentrations of ammonia to be greater than concentrations of ammonia that we found in surface waters in the spring. Brickell and Goering concluded that the ammonia was from the decaying carcasses and not from excretion by pre-eyed salmon eggs. Pre-eyed salmon eggs have low ammonia-excretion rates (Rice and Stokes 1975; Bailey et al. 1980). Unfortunately, no samples of intragravel water were measured in the study by Brickell and Goering, but the potential for harm to developing eggs is probably low because pink salmon eggs are quite tolerant of ammonia at this life stage (Rice and Bailey 1980). In early spring when water flows are low and excretion rates of developing alevins are maximum, high concentrations of ammonia could result. We found concentrations of ammonia in some of the salmon redds to be higher than the concentrations in concurrent samples of surface water and even higher than the concentrations reported by Brickell and Goering in the surface water in the fall.

Although the probability of exposure to high levels of ammonia in spawning grounds is greatest in the spring when alevins are most sensitive, the highest level we observed was below dangerous levels. The highest concentration of ammonia that we found in the intragravel samples was 0.24 ppm total ammonia, which is about 0.1 ppb of toxic un-ionized ammonia at the pH and temperature of Sashin Creek. This concentration is only about one-tenth of the lowest concentration that affected the size of fry resulting from alevins exposed to ammonia for 61 days (Rice and Bailey 1980) and about two-thirds of the maximum concentration found in hatchery incubators containing unusually high densities of eggs (Bailey et al. 1980). Our highest value for intragravel water exceeded the highest concentrations found in surface water of Sashin Creek (Brickell and Goering 1972) when many decaying salmon carcasses were present.

In subarctic and arctic streams where water temperature and pH are low, it seems unlikely that ammonia will accumulate in intragravel waters to concentrations that will significantly affect size or survival of salmon alevins. Ammonia toxicity may be significant at higher temperatures, especially in more alkaline streams.

Acknowledgments

Howard Sears helped us collect the water samples, and William R. Heard and Roy Martin located the random sites and determined the density of alevins at each site.

Literature Cited

BAILEY, J. E., S. D. RICE, J. J. PELLA, AND S. G. TAYLOR.
1980. Effects of seeding density of pink salmon, *Oncorhynchus gorbuscha*, eggs on water chemistry, fry characteristics, and fry survival in gravel incubators. Fish. Bull., U.S. 78:649-658.

BRICKELL, D. C., AND J. J. GOERING.
1972. Chemical effects of salmon decomposition on aquatic ecosystems. *In* R. S. Murphy and D. Nyquist (editors), International Symposium on Water Pollution Control in Cold Climates, p. 125-138. U.S. Gov. Print. Off., Wash., D.C.

MCNEIL, W. J.
1962. Variations in the dissolved oxygen content of intragravel water in four spawning streams of southeastern Alaska. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 402, 15 p.
1964. A method of measuring mortality of pink salmon eggs and larvae. U.S. Fish Wildl. Serv., Fish. Bull. 63:575-588.

MCNEIL, W. J., R. A. WELLS, AND D. C. BRICKELL.
1964. Disappearance of dead pink salmon eggs and larvae from Sashin Creek, Baranof Island, Alaska. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 485, 13 p.

PENAZ, M.
1965. Influence of ammonia on eggs and spawns of stream trout *Salmo trutta* M. Fario. Zool. Listy, Folia Zool. 14:47-53. [Translated by and available from Foreign Fisheries (Translations), U.S. Dep. Commer., Wash., D.C.]

RICE, S. D., AND J. E. BAILEY.
1980. Survival, size, and emergence of pink salmon, *Oncorhynchus gorbuscha*, alevins after short- and long-term exposures to ammonia. Fish. Bull., U.S. 78:641-648.

RICE, S. D., AND R. M. STOKES.
1975. Acute toxicity of ammonia to several developmental stages of rainbow trout, *Salmo gairdneri*. Fish. Bull., U.S. 73:207-211.

U.S. ENVIRONMENTAL PROTECTION AGENCY.
1974. Methods for chemical analysis of water and wastes. U.S. Environ. Prot. Agency, EPA-625-16-74-003, 298 p., Wash., D.C.

VAUX, W. G.
1968. Intragravel flow and interchange of water in a streambed. U.S. Fish. Wildl. Serv., Fish. Bull. 66:479-489.

STANLEY D. RICE
JACK E. BAILEY

Northwest and Alaska Fisheries Center
Auke Bay Laboratory
National Marine Fisheries Service, NOAA
P.O. Box 155
Auke Bay, AK 99821

EGG CANNIBALISM IN THE NORTHERN ANCHOVY, *ENGRAULIS MORDAX*

Anchovies feed on their own eggs. Egg cannibalism has been reported for the Argentine anchovy, *Engraulis anchoita* (de Ciechomski 1967); Japanese anchovy, *E. japonicus* (Hayasi 1967); anchoveta, *E. ringens* (Rojas de Mendiola et al.[1]); and the northern anchovy, *E. mordax* (Loukashkin 1970). These studies give no indication whether this cannibalism was a significant part of natural mortality and incidence of cannibalism was included only as part of a general description of food habits. We provide evidence that egg cannibalism may account for a considerable proportion of natural egg mortality in the northern anchovy.

Northern anchovy feed by biting larger prey and by filtering smaller ones (Leong and O'Connell 1969). If both large and small prey are offered in the laboratory, northern anchovy in the front of the school bite the larger prey, whereas those at the end of the school feed by filtering the smaller prey (O'Connell 1972). Our laboratory observations indicate that adult northern anchovy feed on their eggs by filtering, whereas even the smallest anchovy larvae (ca. 3-4 mm long) are bitten. Such small larvae are digested beyond identification in 30 min, whereas the identifiable whole chorions and fragments may remain in northern anchovy stomachs up to 8 h although the contents of the egg (embryo and yolk) are digested after about 2 h. Northern anchovy eggs are prolate spheroids and can be easily distinguished from the spherical eggs of other pelagic spawners in the Southern California Bight.

Methods

The incidence of cannibalism in northern anchovy was estimated from an examination of 31 sets of stomach samples, usually of 10 adults each. Samples were taken at the peak of the spawning season, in the Southern California Bight, during March 1976 and 1977 (Table 1). Northern anchovy were collected in a midwater trawl or a commercial lampara net; 28 sets of collections were taken at night between sunset and sunrise and 3 sets during the day. Fish were frozen in liquid nitrogen

[1] Rojas de Mendiola, B., N. Ochoa, R. Calienes, and O. Gomez. 1969. Contenido estomacal de anchoveta en cuarto areas de la costa Peruana. Inst. Mar. Peru Inf. Espec. (IM-27), 29 p.

TABLE 1.—Incidence of anchovy eggs in stomachs of northern anchovy collected in March 1976 and 1977 in the Los Angeles Bight.

Time of day (h)	Collection number[1]	Number fish per collection	Mean standard length (cm)	Mean weight (g)	Mean percentage full[2]	Fish with eggs (%)	Mean number eggs per fish
1300	31	25	10.0	10.2	7	68	1.9
1500	29	23	11.7	17.9	13	96	8.4
1500	30	11	12.4	19.9	14	100	6.4
2000	4	10	13.4	22.7	18	50	2.0
2000	5	10	13.4	23.3	18	10	0.1
2000	7	20	13.4	24.9	12	5	1.0
2000	17	10	10.5	11.7	17	30	.7
2100	1	11	10.7	10.0		82	2.3
2100	8	10	13.5	25.4	15	0	.0
2100	10	10	10.5	12.5		100	3.8
2100	14	10	11.6	16.2	49	40	0.6
2100	20	10	11.4	15.0	32	20	0.2
2100	23	10	12.1	19.1	38	0	.0
2200	6	10				20	0.2
2200	9	10	13.7	28.5	13	40	0.9
2200	15	10	11.4	15.9	56	50	7.1
2200	18	10	11.9	17.9	18	70	4.9
2300	11	10	11.4	16.5	14	10	0.1
2300	21	10	12.1	17.9	39	0	.0
2300	24	10	11.8	18.4	35	20	0.2
2400	2	10	10.6	12.2	4	50	3.0
2400	16	10	11.2	14.2	17	60	11.3
2400	19	10	11.5	15.3	15	90	4.6
0100	12	10	11.8	16.7	13	70	2.1
0100	13	10	11.1	14.7	25	90	22.1
0100	25	10	12.9	23.4	30	0	.0
0200	3	28	9.0	7.9	4	86	39.0
0400	27	10	12.0	17.9	31	90	20.9
0500	22	10	12.3	19.4	18	20	0.4
0500	26	10	12.3	19.3	28	30	0.9
0700	28	10	11.6	16.3	20	50	1.7
Means ± 2 SE of mean:							
Night (N = 28)			11.8± .04	17.5± 1.8	23± 4	42± 12	4.6± 3.3
Day (N = 3)			11.4± 1.4	16.0± 5.9	12± 5	88± 20	5.6± 3.5

[1] Collections 1-9, night trawls, March 1976; collections 10-25, night trawls, March 1977; collections 26-28 night lampara sets, March 1977; and collections 29-31 day lampara sets, March 1976.
[2] Volume stomach contents/volume maximum contents × 100. Maximum stomach volume was size specific and derived from the relationship developed in the text.

at the time of capture, except for the day collections where formaldehyde preservation was used.

A standard oblique plankton tow (Smith and Richardson 1977) from 70 m (depth of water permitting) to the surface, was taken before and after each night trawl sample using a 1 m ring net (505 μm mesh) or Bongo net (333 μm mesh) and was preserved in 10% Formalin.[2] The 505 μm mesh net was corrected for extrusion of eggs using the coefficient of Lenarz (1972). These collections were used to estimate the abundance of northern anchovy eggs in the regions where anchovy were sampled by night trawls. For one of the day samples, two plankton tows were taken in front and two taken behind the school. The plankton samples were taken with a 0.5 m ring net with 102 μm mesh, towed for 2 min at 15 m (the depth of the school as determined acoustically). These two sets of plankton samples enabled us to measure directly the effect of feeding by a school on the egg density. No plankton tows were associated with the commercial lampara net samples.

For each fish we determined standard length (SL) and weight, numbers of eggs and larvae in the stomach, and compacted stomach volume. The stomach volume was compacted by centrifuging the contents for 6 min at 3,700 r/min and then was measured to the nearest 0.1 ml. Volumes were expressed as a percentage of the maximum stomach volume. Maximum volume (V) was determined using the same volumetric technique for northern anchovy fed to satiation with adult *Artemia salina* in the laboratory; it was expressed as a function of standard length (L) in centimeters, where $\ln V = 2.051 \ln L - 3.954$ and $r^2 = 0.759$. The length range was 4.6-13.5 cm.

To estimate the ration from observed incidence of eggs in the stomach, the rate of gastric evacuation of eggs must be known. To estimate this rate, we fed only northern anchovy eggs to 155 northern anchovy for 1 h at a density of 38 eggs/l at 15.2° C, which approximates typical spawning temperatures. After feeding, fish were transferred to a tank without food and 10-15 fish sampled at 2-h intervals until 10 h after feeding. The rate of gastric evacuation was expressed as the slope of the regression of natural logarithm of the mean

[2] Use of trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

eggs in the stomach as a function of elapsed time (Figure 1).

Incidence of Cannibalism

No relationship existed between the volume of the stomach contents and the time of collection, indicating that anchovy fed throughout the night and day (Table 1). In the night samples, the mean stomach volume was 23% of that of a full stomach and was 12% in the 3 day samples. Nearly all stomachs contained greenish to brownish material, presumably phytoplankton remains, and somewhat less frequently copepods and euphausiids were mixed with this material.

Larval fishes occurred in only 7 of the 368 stomachs (2%) and only 1 stomach contained larvae that could be identified as northern anchovy. This stomach contained 21 relatively large northern anchovy larvae; the only measurable specimen was 17 mm SL. Northern anchovy eggs occurred more frequently than larvae. Forty-two percent of the northern anchovy stomachs sampled at night contained northern anchovy eggs and 88% of those sampled in the day contained eggs. Other fish eggs were rare, occurring in 4.2±2.7 (±2 SE) of the stomachs. The mean number of anchovy eggs per stomach, including zeros, was 4.6±3.3 (±2 SE) for night samples, 5.6±3.5 for day samples, and the mean for night and day was 5.1 eggs/stomach.

The distribution of the number of eggs consumed per fish was highly skewed; about 90% of the eggs occurred in only 38% of the stomach samples containing eggs (19% of all stomachs). The maximum number of eggs in a single stomach was 730, which was about 32% of all the eggs found in stomachs. The patchiness of northern anchovy eggs in the sea may be responsible for this skewed distribution. The distribution was not greatly different from that of northern anchovy eggs taken in plankton samples. For example, Smith[3] found that about 90% of northern anchovy eggs occurred in only 20% of the positive plankton net hauls (N = 453).

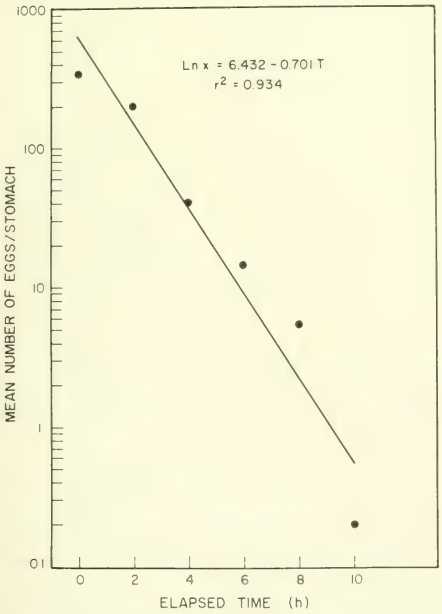


FIGURE 1.—Rate of gastric evacuation of northern anchovy fed northern anchovy eggs. Points are $\log_e$ mean number of eggs per stomach for 10-15 fish sampled at 2-h intervals after feeding.

The mean number of eggs per fish in a sample (night trawl samples) increased with egg density in the sea (Figure 2). Although variability was high (r^2 = 0.47), the 99% confidence interval about the regression coefficient was 1.107-2.095 and did not include a coefficient value of 1. This indicates that the relation was exponential and that the mean number of eggs in the stomach was not increasing in direct proportion to the mean egg abundance. Patchiness of eggs combined with selectivity in filtering could explain the exponential nature of the relationship. Certainly, oblique net tows provided only a relative measure of egg density encountered by filtering northern anchovy. Tows were begun at 70 m (below the maximum depth of northern anchovy larvae (Hunter and Sanchez 1977), or in shallow water near the bottom to insure that all eggs in the water column were sampled. Stomach contents, on the other hand, would be expected to be more closely related to the size of patches and density of eggs within egg patches and not to the integrated egg density for the water column.

Measurements of the density of eggs behind and in front of a single northern anchovy school were probably a more realistic measurement of the

[3] P. E. Smith, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun. December 1979.

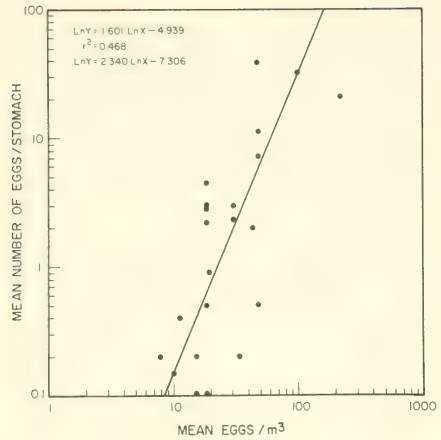


FIGURE 2.—Mean density of northern anchovy eggs in the sea and mean number of eggs in northern anchovy stomachs taken in the Los Angeles Bight in March 1976 and 1977. Points are means for 10 or more fish and means of 2-4 plankton tows. Upper equation and the line is the geometric mean regression (Ricker 1973); lower equation is the predictive equation.

actual density of eggs encountered by a school. These measurements were derived from horizontal tows made at the acoustically determined depth of the school (15 m). Estimates from the two tows taken in front of the school were 150 and 122 eggs/m^3, whereas those from the two tows taken behind the school were 75 and 54 eggs/m^3. The ratio of the means for these two sets (65:136) indicated that 48% of the eggs in the water may have been consumed by the school. Thus, a school encountering a density of about 140 eggs/m^3 may have consumed a large proportion of the eggs. The density of eggs usually encountered by schools during the peak spawning months may be in excess of 140 eggs/m^3 because the mean number of eggs per stomach for fish in this school, 1.9 ± 0.6 eggs (Collection 31, Table 1) was less than the mean for all collections, 5.1. The typical density of northern anchovy eggs within patches is not known, but a value as high as 31,000 eggs/m^3 has been recorded (Hunter in press).

The daily ration of eggs consumed by northern anchovy was estimated from the equation, $D = A \times B \times C$ where D = ration (number of eggs), B = rate of gastric evacuation (0.701), A = mean stomach contents, and C = duration of feeding (24 h). This function has been used by Tyler (1970), discussed and used by Eggers (1977), and criticized and discussed by Elliott and Persson (1978). We used for mean stomach contents (C), the mean of the averages for day and night. Using the above equation, the daily ration was 85.8 eggs/fish or 5.1 eggs/g of fish (Table 2).

The simplest method for evaluating potential effects of egg consumption is to calculate the proportion of the nightly production of eggs consumed by northern anchovy schools. Northern anchovy produce 371 eggs/g of female per spawning and during peak breeding periods, about 16% of the females spawn each night (Hunter and Goldberg 1980). Thus each night, 0.16 × 371, or 59.4 eggs are spawned per gram of female in a school. Assuming a sex ratio of 1:1, half this amount, or 29.7 eggs, are produced per gram school weight. The percentage of daily egg production consumed by a school per day (eggs consumed/eggs spawned) was 17.2% (Table 2). Smith (footnote 3) estimated the natural mortality of anchovy

TABLE 2.—Number of anchovy eggs eaten, per day, proportion of egg production consumed, and the proportion of natural egg mortality attributable to egg cannibalism in northern anchovy.

	Variable	Value	SE of mean	Data source
A	Mean eggs/stomach	5.1	[1] ± 1.6	Mean of night and day averages (Table 1)
B	Rate of gastric evacuation	.701	± 0.092	See text
C	Duration of feeding (h)	24		
D	Ration, eggs/fish per day	85.80		A × B × C
E	Mean fish weight (g)	16.8	[1] ± 0.9	Mean of night and day averages (Table 1)
F	Ration, eggs/grams wet weight	5.1		D/E
G	Eggs spawned/grams ovary-free female weight	389	± 30	Hunter and Goldberg 1980
H	Ratio of ovary-free weight to total female weight	.954		Hunter and Macewicz[2]
I	Eggs spawned/grams total female weight	371	± 28	G × H
J	Ratio of females spawning/night	.16	± 0.02	Hunter and Goldberg 1980
K	Ration of females/school	.50		Assumed 1:1 sex ratio
L	Eggs/gram school weight	29.7		I × J × K
M	Percent of egg production consumed/day	17.2		F/L
N	Natural egg mortality percentage/day	53		Smith and Lasker 1978
O	Percentage natural mortality from cannibalism	32.4		M:N

[1] From the night samples, Table 1.
[2] Hunter, J. R., and B. J. Macewicz. 1979. Sexual maturity, batch fecundity, spawning frequency, and temporal pattern of spawning northern anchovy, *Engraulis mordax*, during the 1979 spawning season. Manuscript submitted for publication.

eggs to be about 53%/d. Thus, egg cannibalism may be the cause of 32% of the natural egg mortality in northern anchovy.

Discussion

We have not tried to trace the error terms through the pyramid of calculations required to estimate the proportion of natural egg mortality attributable to cannibalism, although we give in Table 2 the standard error of the mean where estimates are available. The error in our estimate most likely will be equivalent or higher than that of the most variable parameter (i.e., mean eggs per stomach and natural mortality of northern anchovy eggs). We have no estimate of the error for the natural mortality of northern anchovy eggs but mortality rates of pelagic fish eggs are known to be high and variable; estimates range from 2 to 95% for various species (Jones and Hall 1974; Vladimirov 1975). Regardless of the uncertainties, we believe the results indicate that egg cannibalism may be a major source of egg mortality in the northern anchovy and a combination of patchiness of eggs and selectivity in filter feeding may be important in regulating the consumption of eggs.

Cannibalism is a mechanism for density-dependent regulation of fish populations (Cushing 1977), and egg cannibalism may be one of the many mechanisms regulating the size of anchovy populations. A simple model could be developed to test this hypothesis if random filtering and a random egg distribution were assumed. Although the development of such a model is beyond the scope of this paper, we wish to consider the extent our observations differ from predictions based on assumptions of randomness because this would be a critical decision in the development of the model.

The mean density of eggs in trawl associated plankton tows was 32 eggs/m^3 and the maximum filtering rate of northern anchovy of mean weight 16.8 g, is 0.158 m^3/h (Leong and O'Connell 1969). For a northern anchovy (weight 16.8 g) to obtain the estimated ration of 85.8 eggs/d, it would have to filter continuously for 17 h at a density of 32 eggs/m^3. Another approach is to estimate the percentage of the volume of the habitat that could be randomly filtered by a group of northern anchovy schools. The mean weight of northern anchovy schools in 20′ grid squares is 2.05×10^7 kg (excluding grid squares without northern anchovy) (Mais[4]); assuming the maximum depth of eggs is 30 m (Hunter and Sanchez 1977), the volume of the habitat is 2.86×10^{10} m^3. These schools would have to filter for 24 h to consume 17% of the nightly egg production. The number of hours of filtering required to obtain the average daily ration of eggs in the first calculation or to consume 17% of the egg production in the second is too high. Thus a random encounter model does not seem to account for the relatively high egg consumption that was observed and patchiness and selectivity in feeding may be the reasons.

Northern anchovy eggs exist in patches (Hewitt in press), probably in patterns similar to those described for sardine eggs (Smith 1973). Our observations of northern anchovy feeding on eggs in the laboratory indicate that filtering may be intensified when egg patches are encountered. When we added a beaker containing anchovy eggs to a 3.3 m diameter tank containing about 200 northern anchovy, they soon interrupted their circuit of the tank, formed a tight mill at the site of introduction, and filtered the region intensively. If northern anchovy display such patterns of behavior in the sea, the ration of eggs would be expected to be higher than one predicted from random filtering. Thus, present evidence indicates that an assumption of randomness would be unacceptable in a model to measure effects of cannibalism as a regulatory mechanism.

Larval cannibalism might also be significant. Northern anchovy larvae are readily eaten by adults in the laboratory. The absence of small northern anchovy larvae in stomachs may have been caused by the rapid rate of digestion (<30 min) and the low incidence of larger larvae (0.3%) caused by their low abundance in the sea. Thus, cannibalism on larvae as well as that on eggs might play a role in the regulation of northern anchovy populations but additional information is needed on feeding behavior, and on the size and density of egg and larval patches, before an evaluation of population effects can be made.

Acknowledgments

Sharon Hendrix and Harold Dorr (Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla, Calif.) assisted in collection and processing of adult northern anchovy samples. Daylight trawl collections and associated plankton tows were made by Anthony Koslow (Scripps

[4]Mais, K. F. California Department of Fish and Game, Cruise Reports 76-A-3 and 77-A-3. California Department of Fish and Game, Marine Resources Region, Long Beach, Calif.

Institution of Oceanography, University of California at San Diego, La Jolla). Alec MacCall (California Department of Fish and Game, La Jolla) gave helpful suggestions regarding the interpretation of the results.

Literature Cited

CUSHING, D. H.
1977. The problems of stock and recruitment. *In* J. A. Gulland (editor), Fish population dynamics, p. 116-133. Wiley, N.Y.

CIECHOMSKI, J. D. DE
1967. Investigations of food and feeding habits of larvae and juveniles of the Argentine anchovy *Engraulis anchoita*. Calif. Coop. Oceanic Fish. Invest. Rep. 11: 72-81.

EGGERS, D. M.
1977. Factors in interpreting data obtained by diel sampling of fish stomachs. J. Fish. Res. Board Can. 34: 290-294.

ELLIOTT, J. M., AND L. PERSSON.
1978. The estimation of daily rates of food consumption for fish. J. Anim. Ecol. 47:977-991.

HAYASI, S.
1967. A note on the biology and fishery of the Japanese anchovy, *Engraulis japonica* (Houttuyn). Calif. Coop. Oceanic Fish. Invest. Rep. 11:44-57.

HEWITT, R.
In press. The value of pattern in the distribution of young fish. *In* R. Lasker and K. Sherman (editors), The early life history of fish. II. A Second International Symposium held in Woods Hole, 2-5 April 1979. Rapp. P.-V. Réun. Cons. Int. Explor. Mer. 178.

HUNTER, J. R.
In press. The feeding behavior and ecology of marine fish larvae. *In* J. E. Bardach (editor), The physiological and behavioral manipulation of food fish as production and management tools. International Center for Living Aquatic Resources Management, Manila.

HUNTER, J. R., AND S. R. GOLDBERG.
1980. Spawning incidence and batch fecundity in northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 77: 641-652.

HUNTER, J. R., AND C. SANCHEZ.
1977. Diel changes in swim bladder inflation of the larvae of the northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 74:847-855.

JONES, R., AND W. B. HALL.
1974. Some observations on the population dynamics of the larval stage in the common gadoids. *In* J. H. S. Blaxter (editor), The early life history of fish, p. 87-102. Springer-Verlag, N.Y.

LENARZ, W. H.
1972. Mesh retention of larvae of *Sardinops caerulea* and *Engraulis mordax* by plankton nets. Fish. Bull., U.S. 70:839-848.

LEONG, R. J. H., AND C. P. O'CONNELL.
1969. A laboratory study of particulate and filter feeding of the northern anchovy (*Engraulis mordax*). J. Fish. Res. Board Can. 26:557-582.

LOUKASHKIN, A. S.
1970. On the diet and feeding behavior of the northern anchovy *Engraulis mordax* (Girard). Proc. Calif. Acad. Sci., Ser. 4, 37:419-458.

O'CONNELL, C. P.
1972. The interrelation of biting and filtering in the feeding activity of the northern anchovy (*Engraulis mordax*). J. Fish. Res. Board Can. 29:285-293.

RICKER, W. E.
1973. Linear regressions in fishery research. J. Fish. Res. Board Can. 30:409-434.

SMITH, P. E.
1973. The mortality and dispersal of sardine eggs and larvae. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 164: 282-292.

SMITH, P. E., AND R. LASKER.
1978. Position of larval fish in an ecosystem. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 173:77-84.

SMITH, P. E., AND S. L. RICHARDSON.
1977. Standard techniques for pelagic fish egg and larva surveys. FAO Fish. Tech. Pap. 175, 100 p.

TYLER, A. V.
1970. Rates of gastric emptying in young cod. J. Fish. Res. Board Can. 27:1177-1189.

VLADIMIROV, V. I.
1975. Critical periods in the development of fishes. J. Ichthyol. 15:851-868. (Engl. transl. of Vopr. Ikhtiol.)

JOHN R. HUNTER
CAROL A. KIMBRELL

Southwest Fisheries Center La Jolla Laboratory
National Marine Fisheries Service, NOAA
P.O. Box 721
La Jolla, CA 92038

DEPTH DISTRIBUTION AND SEASONAL AND DIEL MOVEMENTS OF RATFISH, *HYDROLAGUS COLLIEI*, IN PUGET SOUND, WASHINGTON[1]

The ratfish, *Hydrolagus colliei*, inhabits the coastal waters of North America from Alaska to the Gulf of California (Hart 1973). One aspect of the biology of this species which has attracted attention is its vision physiology. It is generally accepted that most deepwater fish, regardless of phylogenetic position, have retinal pigments with maximum absorption at about 490 nm or less (Munz 1971; Lythgoe 1972). For example, *H. affinis*, the species of chimaeroid found in deep water of the western Atlantic, has retinal pigments with maximum absorbance at 477 nm (Denton and Nicol 1964). In contrast, a shallow-water species of chimaeroid (*Callorhinchus callorhynchus*) found off Chile has retinal pigments with

[1]Contribution No. 514 College of Fisheries, University of Washington, Seattle, Wash.

maximum absorbance at 499 nm, a value which is typical of coastal fishes (McFarland 1970). Crescitelli (1969) and Beatty (1969), however, have reported that *H. colliei*, which can occur in water only 5 m deep, possesses retinal pigments characteristic of deepwater fish (λ_{max} = 484 nm). Crescitelli (1969) remarked that it is anomalous to find such pigments in a coastal species.

Like the retinal pigments, the structures for regulating the amount of light striking the retina in this species seem to be adapted to deep water. Maddock and Nicol (1978) found that the pupils of *H. colliei* cannot be contracted in bright light, and the reflective tapetum lucidum has no movable layer of dark pigments to eliminate eyeshine in bright light. While Stell[2] has found that there is an increase in pigmentation on the tapetum after full light adaptation, he estimated the degree of occulsion at 20% or less. Stell also indicated that ratfish appear to have an all-rod retina, a further adaptation to low light levels. In attempting to relate the spectral sensitivity of chimaeroid retinal pigments to depth of occurrence, Crescitelli (1969) and McFarland (1970) both noted that the absence of behavioral or ecological data on *H. colliei* makes it difficult to classify this species as an inhabitant of deep, shallow, or intermediate depths.

In the Gulf of California, *H. colliei* is typically captured below 275 m, although abundance varied seasonally (Matthews 1975). In other parts of its geographic range this species clearly inhabits shallower water. Jopson (1958) observed ratfish trapped in tide pools on the Oregon coast, and Dean (1906) reported catching them in about 4 m of water in Port Townsend Bay, Wash.

Recent studies have suggested that ratfish may undergo diel onshore migrations in Puget Sound. Miller et al.[3] reported trammel net catches of ratfish at night in areas where none were observed by scuba divers during the day. Moulton (1977) observed ratfish only in the evening and at night during dives on rocky reef sites. However, other divers (unpubl. obs.) have reported occasional sightings of ratfish in shallow water during the day.

To further understand the relationship between visual systems and fish depth distribution, the present study was designed to focus on three questions. First, what is the overall bathymetric distribution of ratfish in Puget Sound? Second, to what extent do Puget Sound ratfish undergo seasonal and diel onshore migrations? Third, is there evidence for size- or sex-related patterns of abundance or movements?

Methods

Seven sites in central Puget Sound were sampled between 1965 and 1978: Port Madison, Port Gardner, Mukilteo, Duwamish Head, Point Pully, Alki Point, and West Point (Figure 1). Samples were obtained with a 6 m otter trawl and a 6 m beam trawl which we have previously found to fish with approximately the same results. All tows were on the bottom for 5 min.

FIGURE 1.—Map of Puget Sound, Wash., with sites where ratfish were sampled. 1, Eagle Cove; 2, Port Townsend Bay; 3, Port Gardner; 4, Mukilteo; 5, Port Madison; 6, West Point; 7, Duwamish Head; 8, Alki Point; 9, Point Pully.

[2]William K. Stell, Professor of Ophthalmology and Anatomy, Jules Stein Eye Institute, University of California, Los Angeles, Los Angeles, CA 90024, pers. commun. January 1978.

[3]Miller, B. S., C. A. Simenstad, and L. L. Moulton. 1976. Puget Sound baseline program: Nearshore fish survey. Unpubl. manuscr., 196 p. Univ. Wash., Fish. Res. Inst. FRI-UW-7604.

All sites were sampled during daylight hours about once a month. The depths sampled varied among the areas, but all sites were sampled at discrete depths between 10 and 70 m, several were sampled between 10 and 120 m, and one site between 5 and 150 m. When considering seasonal changes, winter was defined as January-March, spring as April-June, summer as July-September, and fall as October-December. Sampling effort was essentially the same at a given site and depth over all seasons.

Diel (24-h) studies were conducted at West Point in central Puget Sound (Figure 1) on 4 Nov. 1975, 13 Feb. 1976, 15 May 1976, 20 Aug. 1976, 19 Nov. 1976, and 5 May 1978. These six studies involved sampling at depths of 5, 15, 25, 35, 45, and 55 m every 4 h. The data were grouped into six time periods (Pacific standard time): 0400-0800, 0800-1200, 1200-1600, 1600-2000, 2000-2400, and 2400-0400 h.

In addition to the major sampling effort at the seven sites, a 24-h study was conducted at Eagle Cove (San Juan Island) in northern Puget Sound, and some daytime sampling was conducted in Port Townsend Bay (Figure 1).

All ratfish were counted, and length (measured to the end of the second dorsal fin), weight, and sex recorded.

Results

When all months were combined, data from the seven principal sampling sites indicated that ratfish were most abundant in the 55-95 m depth range. Hauls from depths <50 m and >100 m generally had a lower catch per unit effort of ratfish than those made at intermediate depths (Figure 2).

Port Townsend Bay was an exception to this pattern. Ratfish from this shallow-depth area (< 30 m) were sampled during June, August, and September 1978. In a total of 60 hauls at depths from 3 to 27 m, 182 ratfish were caught. This relatively high abundance of ratfish (3.03 fish/haul) in shallow water was in direct contrast to the scarcity of ratfish in <30 m at the other sites (1.31 fish/haul). (Actually, this latter average may be inflated by a few abundant hauls at Port Madison in the spring. If the Port Madison hauls are omitted, the average drops to 0.70 fish/haul). Not only was there an unusually large number of ratfish in shallow Port Townsend Bay, but the fish seemed to be selecting shallower water within the bay, because peak catches occurred in water only 10 m deep.

With the exception of the Port Townsend Bay samples, the basic depth distribution pattern was similar at the seven major sites. However, the pattern was subject to seasonal and diel variations. Catch per unit effort of ratfish was generally highest in spring, declined during summer and fall, and increased again in winter (Figure 3). This pattern was matched by a minimum average depth of capture in spring (70.5 m) and a maximum

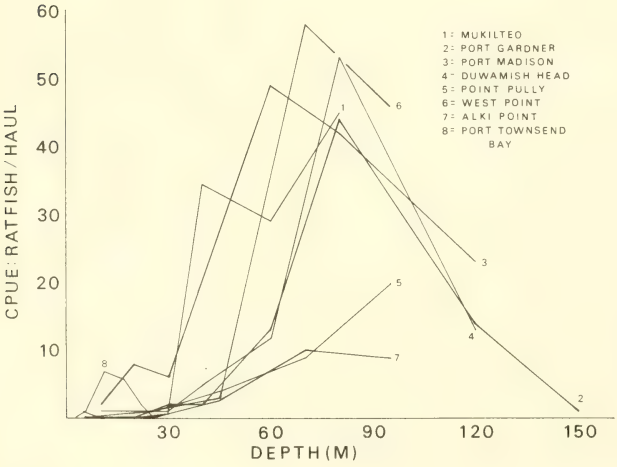


FIGURE 2.—Daytime depth distribution of ratfish at eight sites in Puget Sound, Wash., throughout the year.

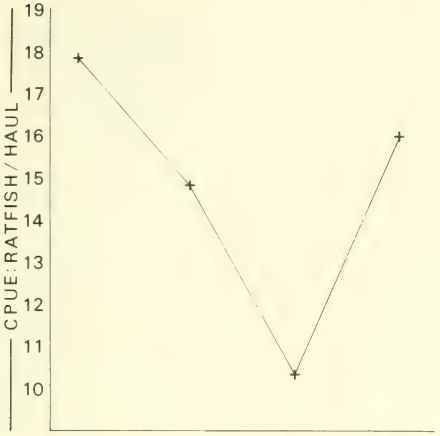


FIGURE 3.—Seasonal relationship between ratfish abundance (CPUE, catch per unit effort) in Puget Sound, Wash. (data averaged for the seven principal sites).

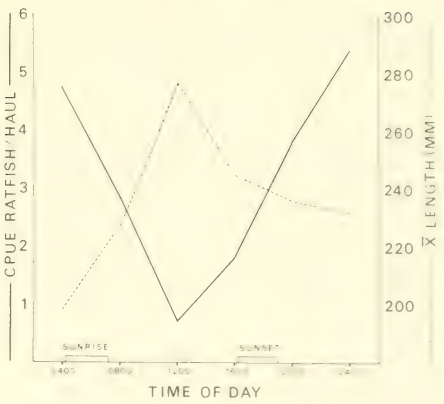


FIGURE 4.—Diel changes in abundance (CPUE, catch per unit effort) and average size of ratfish caught in shallow water (5-55 m) at West Point, Puget Sound, Wash.; data averaged from six 24-h studies.

average depth of capture in the fall (76.5 m). These two trends indicate that ratfish move shallower in the spring and deeper in the fall, perhaps beyond the sampling range of this study.

The 24-h studies gave evidence of a nocturnal, onshore movement. Within the sampling depths of 5-55 m, the number of fish per haul ranged from 0.69 in the 1200-1600 sample series to 5.42 in the 2400-0400 series (Figure 4). Although the samples were taken at different times of year, sunrise was always between 0415 and 0715 h, and sunset was between 1615 and 1930 h on the dates when the sampling was done. The data from the 24-h study at Eagle Cove also showed a peak in nearshore abundance after sunset and before sunrise, consistent with the West Point data.

The 24-h studies also provided evidence that large and small ratfish were not behaving alike. Although large fish were caught at night, there was a decrease in average length (Figure 4) indicating that the nocturnal onshore migration was composed principally of small fish.

Analysis of the combined monthly data from West Point, Alki Point, and Point Pully indicated that fish caught in shallow water were larger than those caught in deeper water (Figure 5). This trend was also apparent for the West Point 24-h and Port Townsend Bay data as well. The samples at Port Townsend Bay were from water <30 m

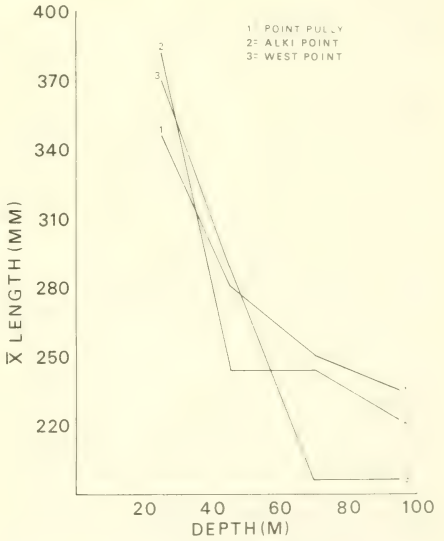


FIGURE 5.—Relationship between depth of capture and ratfish length in samples from three sites in Puget Sound, Wash.

deep, and the average length was 360 mm (±74 mm SD), and no ratfish were <200 mm long.

Sex ratios of ratfish at West Point, Alki Point, and Point Pully were significantly (chi-square)

different from 1:1 ratio only in the spring, when 60% of the ratfish caught were females.

Discussion

In Puget Sound, the ratfish was most abundant from 55 to 99 m. While it should be noted that only three sites were sampled below 100 m, and none below 150 m, most of Puget Sound proper is shallower than 150 m. Still, the depth distribution of ratfish in central Puget Sound differs from that in the Gulf of California (Matthews 1975).

These southern ratfish were most abundant from 257 to 400 m. After noting a peak of abundance in February, Matthews (1975) speculated that the ratfish move into very deep water during the summer and fall, and return to shallower water in the winter and spring. This would be generally similar to the seasonal pattern of abundance observed at the Puget Sound sampling sites, where maximum abundance was in the spring (April-June); later in the year, the fish were in slightly deeper water.

While the differences in overall depth distribution of the Puget Sound and Gulf of California populations may be temperature related, and the seasonal movements may be related to reproduction, these factors do not seem to explain the diel movements of the Puget Sound population. One possible explanation for the nocturnal onshore movements of Puget Sound ratfish is that there is some food resource which is being exploited in shallow water. A study of ratfish food habits off the Oregon coast (Johnson and Horton 1972) found that 75% of the food items consumed were *Amphissa* sp., a gastropod mollusc. A study of ratfish food habits from Puget Sound indicates a much less specialized diet. Stomachs from 71 West Point ratfish contained a wide variety of items (Wingert et al.[4]). In general, smaller ratfish (<200 mm) fed principally on polychaetes, but stomachs of larger ratfish contained primarily bivalves, fish, and decapods. While some food items such as limpets and barnacles indicated shallow-water feeding, the sample size was not sufficient to establish the main feeding times or depths. Miller et al.[5] and Fresh et al.[6] also found wide prey spectra, with fish and polychaetes being the most important items. Ratfish seems to feed opportunistically on the most abundant, available items and will eat a wide range of crustaceans, molluscs, annelids, fish, echinoderms, and algae.

Whether or not the onshore movements are food-oriented, we still must explain why most of the small ratfish are found in deep water, and why they apparently approach shore primarily at night. One possible explanation is predator avoidance. The large, poisonous dorsal spine and large size probably make adults relatively safe from predation, but perhaps not juveniles. During the day, juveniles may tend to stay in deep water where their blue-shifted retinal pigment may give them an advantage over potential predators such as spiny dogfish, *Squalus acanthias* (Jones and Geen 1977).

The Puget Sound ratfish population is exploiting a nearshore niche. Its retinal pigment (chrysopsin) and eye morphology are similar to deep-sea chimaeroids, such as *H. affinis*, yet its depth distribution is comparable to many fish with retinal pigments located near 500 mm. By contrast, *C. callorhynchus* seems to be a more well-established coastal chimaeroid, having a typical coastal rhodopsin with peak absorbance at 499 mm (McFarland 1970). However, *H. colliei* has some adaptations to an environment with moderate light levels. Arnott and Nicol (1970) described the histological basis of the reflective skin of the species and explained this sheen as a camouflage device by which the reflected light would match the background illumination. The authors point out that this reflective sheen is typical of chimaeroids from moderate depths, such as *Chimaera monstrosa*, *C. cubana*, *C. phantasma*, and *Callorhinchus callorhynchus*, but that deep-sea members of the group, such as *H. affinis*, have dull-colored skin. Thus, *C. callorhynchus* seems to be well adapted to its nearshore habitat, *H. affinis* is adapted to its deep-sea habitat, and *H. colliei* is partly adapted to deep water and partly to shallow water.

While the visual system of *H. colliei* is clearly suited to the deep distribution exemplified by the Gulf of California population, it also seems com-

[4]Wingert, R. C., C. B. Terry, and B. S. Miller. 1979. Food and feeding habits of ecologically important nearshore and demersal fishes in central Puget Sound. Unpubl. manuscr., 83 p. Univ. Wash., Fish. Res. Inst. FRI-UW-7903.

[5]Miller, B. S., C. A. Simenstad, L. L. Moulton, K. L Fresh, F. C. Funk, W. A. Karp, and S. F. Borton. 1977. Puget Sound baseline program: Nearshore fish survey. Unpubl. manuscr., 220 p. Univ. Wash., Fish Res. Inst. FRI-UW-7710.

[6]Fresh, K. L., D. Rabin, C. A. Simenstad, E. O. Salo, K. Garrison, and L. Matheson. 1978. Fish ecology studies in the Nisqually Reach area of southern Puget Sound, Washington. Unpubl. manuscr., 151 p. Univ. Wash., Fish. Res. Inst. FRI-UW-7812.

patible with the distribution and behavior of Puget Sound ratfish.

While no quantitative measurements were made of light intensity or wavelength, to the human eye, the water in Puget Sound is quite dark at 25 m during the day, especially in winter. Considering that the fish is most abundant at about 75 m during the day and generally moves near shore only at night, McFarland's (1970) assessment that its retinal pigment might be appropriate for its depth distribution seems to be correct. Other aspects of its visual system, such as the apparently all-rod retina and nearly nonocclusible tapetum seem generally appropriate to its observed depth distribution. However, only more extensive studies of the feeding ecology, predators, and possible competitors of ratfish can explain why it moves onshore, why in some areas, such as Port Townsend Bay, it is found in shallow water during the day, and why in general it is found closer to shore in Puget Sound than in other areas in its range.

In summary, the data indicate that in Puget Sound, large ratfish predominate in shallow water, and smaller ones in deeper water. The species is most abundant in about 75 m of water, and tends to be in slightly shallower water in the spring and deeper water in the fall. Ratfish has a pronounced nocturnal onshore movement, which is composed primarily of smaller ratfish from deeper water.

Literature Cited

ARNOTT, H. J., AND J. A. C. NICOL.
1970. Reflection of ratfish skin (*Hydrolagus colliei*). Can. J. Zool. 48:137-151.

BEATTY, D. D.
1969. Visual pigments of three species of cartilaginous fishes. Nature (Lond.) 222:285.

CRESCITELLI, F.
1969. The visual pigment of a chimaeroid fish. Vision Res. 9:1407-1414.

DEAN, B.
1906. Chimaeroid fishes and their development. Carnegie Inst. Wash. Publ. 32, 194 p.

DENTON E. J., AND J. A. C. NICOL.
1964. The chorioidal tapeta of some cartilaginous fishes (Chondrichthyes). J. Mar. Biol. Assoc. U.K. 44:219-258.

HART, J. L.
1973. Pacific fishes of Canada. Fish. Res. Board Can., Bull. 180, 740 p.

JOHNSON, A. G., AND H. F. HORTON.
1972. Length-weight relationship, food habits, parasites and sex and age determination of the ratfish, *Hydrolagus colliei* (Lay and Bennett). Fish. Bull., U.S. 70:421-429.

JONES, B. C., AND G. H. GEEN.
1977. Food and feeding of spiny dogfish (*Squalus acanthias*) in British Columbia waters. J. Fish. Res. Board Can. 34:2067-2078.

JOPSON, H. G. M.
1958. A concentration of the ratfish, *Hydrolagus colliei*, Cape Arago, Oregon. Copeia 1958:232.

LYTHGOE, J. N.
1972. List of vertebrate visual pigments. *In* H. J. A. Dartnall (editor), Photochemistry of vision . Handbook of sensory physiology, Vol. 7, Part 1, p. 604-624. Springer-Verlag, Berl.

MADDOCK, R. G., AND J. A. C. NICOL.
1978. Studies on the eyes of *Hydrolagus* (Pisces: Chimaeridae). Contrib. Mar. Sci. 21:77-87.

MATTHEWS, C. P.
1975. Note on the ecology of the ratfish, *Hydrolagus colliei*, in the Gulf of California. Calif. Fish Game 61:47-53.

MCFARLAND, W. N.
1970. Visual pigment of *Callorhinchus callorhynchus*, a southern hemisphere chimaeroid fish. Vision Res. 10:939-942.

MOULTON, L. L.
1977. An ecological analysis of fishes inhabiting the rocky nearshore regions of northern Puget Sound, Washington. Ph.D. Thesis, Univ. Washington, Seattle, 181 p.

MUNZ, F. W.
1971. Vision: Visual pigments. *In* W. S. Hoar and D. J. Randall (editors), Fish physiology, Vol. 5, p. 1-32. Acad. Press, N.Y.

THOMAS P. QUINN
BRUCE S. MILLER

College of Fisheries
University of Washington
Seattle, WA 98195

R. CRAIG WINGERT

College of Fisheries, University of Washington
Seattle, Wash.
Present address: *Marine Biological Consultants, Inc.*
Costa Mesa, CA 92627

DETECTION OF PETROLEUM HYDROCARBONS BY THE DUNGENESS CRAB, *CANCER MAGISTER*

Behavioral responses that mitigate the effects of natural environmental perturbations may also be effective for contaminants from human activities, but the occurrence of any behavioral response, e.g., avoidance, first requires detection of the contaminant (Olla et al. 1980). To predict whether a behavioral response to a chemical pollutant will occur, one must ask whether the organism can detect the pollutant at concentrations likely to be encountered in field situations. Here we re-

port how antennular behavior was used to determine the concentrations at which the Dungeness crab, *Cancer magister* (Dana), detected petroleum hydrocarbons.

For decapod crustaceans the antennules have been considered the site of distance chemoreception (Hazlett 1971), and their flicking may be analogous to sniffing in vertebrates (Fuzessery 1978). Previous work has shown that in the blue crab, *Callinectes sapidus*, the antennular behavior indicating detection of food substances (Pearson and Olla 1977) also indicated detection of the petroleum hydrocarbon naphthalene (Pearson and Olla 1979, 1980) and the water soluble fraction of crude oil (Pearson et al. in press). In the Dungeness crab, similar antennular behavior, i.e., a change in orientation and increased flicking rate, also indicated detection of food substances (Pearson et al. 1979). Here we used these changes in antennular behavior to determine chemosensory detection thresholds in the Dungeness crab for naphthalene and the water soluble fraction (WSF) of Prudhoe Bay crude oil.

Materials and Methods

Dungeness crabs, trapped in the Strait of Juan de Fuca, Wash., were held outdoors in 1,200 l tanks under the conditions described by Pearson et al. (1979). The seawater temperatures (± SD) during the naphthalene and WSF experiments were 12.7° ± 0.6° C and 10.6° ± 0.3° C; the salinities, 31.6 ± 0.9‰ and 32.0 ± 0.0‰; the dissolved oxygen, 6.9 ± 0.7 mg/l and 7.3 ± 0.5 mg/l; and the pH, 8.12 ± 0.17 and 8.02 ± 0.16.

Experimental Solutions

Saturated solutions of naphthalene were prepared by adding naphthalene crystals to seawater filtered through a 0.4 μm Nucleopore[1] membrane. These stock solutions were stirred continuously at room temperature on a magnetic stirrer and were used after at least 18 h of stirring and no more than 5 d from first use. On each day of testing, a portion of the stock solution was siphoned off and passed through a 100 ml glass syringe fitted with a Millipore prefilter (Type A025) to remove any naphthalene crystals. Less than 1 h before testing, serial dilutions of this filtered stock naphthalene solution were made with seawater freshly filtered through a 0.4 μm membrane. An aliquot of the filtered seawater used for dilution served as the control solution. Experimental and control solutions were kept in a water bath at ambient seawater temperature during testing.

On each day of testing, samples of the stock solution and 10^{-1} dilution were analyzed for naphthalene content. Ten milliliters of hexane were vigorously shaken with 50 ml of sample solution for 1 min. This hexane was removed and analyzed for naphthalene content by capillary GC methods (Bean et al. 1978). The stock naphthalene solution was 22.9 ± 2.1 mg/l, and the 10^{-1} dilution was 2.2 ± 0.2 mg/l.

The WSF of Prudhoe Bay crude oil was prepared freshly each day by methods similar to Anderson et al. (1974). In a 19 l glass bottle, one part oil was gently poured over nine parts membrane-filtered seawater. Before the oil was added, a glass siphon tube inserted through a stopper covered with aluminum foil was placed in the filtered seawater. With the bottle stoppered, the seawater was slowly stirred on a magnetic stirrer for 20 h at room temperature. The stirring speed was adjusted so that the vortex did not extend more than 25% of the distance to the bottom of the bottle. After mixing, the oil and water phases were allowed to separate for 1 h. The water phase was then siphoned from below the oil phase and filtered through a prefilter under very low pressure to remove any remaining oil droplets. Serial dilutions of the resulting WSF were then immediately made with freshly membrane-filtered seawater and kept in a water bath at ambient seawater temperature during use. The membrane-filtered seawater used for dilution was the control solution. The stock WSF was analyzed by capillary gas chromatography for diaromatic and triaromatic hydrocarbons (Bean et al. 1978), and by gas partitioning analysis modified from McAuliffe (1971) for monoaromatics.

Chemosensory Threshold Determination

The apparatus and procedures of Pearson et al. (1979) were used here. In brief, glass testing chambers were arranged on four trays, 10 chambers to a tray, and the trays were surrounded by blinds. The experimental solutions were introduced into each testing chamber through an inlet manifold connected to a glass funnel. Seawater

[1] The use of trademarks does not imply endorsement by National Marine Fisheries Service, NOAA or Battelle, Pacific Northwest Laboratories.

from dripper arms entered each funnel at a rate of 1.0 l/min. A Teflon delivery tube carried the experimental solutions to the funnel from a buret calibrated to deliver 20 ml in 15 s.

To obtain a dilution factor for estimating the effective concentration of experimental solutions within a testing chamber, seawater solutions of ^{14}C-naphthalene (sp. act. 3.6 mCi/mmole, Amersham-Searle Corporation) were introduced and samples taken at timed intervals from the midpoint of the chamber and counted for radioactivity by liquid scintillation spectrometry. The chamber contained a crab model displacing 701 ml, a volume typical of the crabs tested. The maximum concentration in the chamber occurred 45 s after ^{14}C-naphthalene was added and was 0.0188 (± 0.0058 SD) times the concentration of the introduced solution. This dilution factor did not differ significantly from that found by Pearson et al. (1979) using a visible dye.

Approximately 24 h before testing, crabs were transferred to the testing chambers from the holding tanks where they had been fed an ad libitum diet of the blue mussel, *Mytilus edulis*. Because, in preliminary experiments, tidal phase was found to influence chemosensory responses (Pearson et al. 1979), testing was synchronized to begin and end within either a rising or falling tide. The seawater for the test dilutions and control was drawn and filtered 1 h after a tidal change. Testing then began as soon as possible and stopped before the next tidal change.

Each day a maximum of 40 crabs were presented individually with 20 ml of either one of nine dilutions of naphthalene stock solution, one of eight dilutions of WSF, or a control of filtered seawater. Molting and mating crabs were not tested. The order in which individual crabs were watched and the choice of experimental solution were randomized except that active crabs and ones with retracted antennules were passed over. The observer did not know the identity of any test solution. Individual crabs were observed for 1.0 min prior to introduction of the experimental solution, and their antennular flicking rate and other behavior recorded. The flicking rate of one antennule was measured using a hand-held counter. The solution was then introduced, and the observations continued for 1.0 min after the beginning of solution addition. The behavior was scored with the criteria used by Pearson et al. (1979).

To be scored as detecting an experimental solution, a crab had to exhibit an abrupt change in the orientation of the antennules within 30 s after solution introduction, and the ratio of the antennular flicking rate for 1.0 min after solution introduction to that for 1.0 min before had to be 1.50 or above. This value was determined previously by Pearson et al. (1979) from observations of crabs in the testing apparatus without any solutions present. Because 1.50 was the 95th percentile of these antennular flicking rate ratios, the a priori probability that a flicking rate ratio >1.50 represented a spontaneous increase rather than a reaction to the experimental solution was $<5\%$.

Results

Composition of the WSF

The monoaromatic hydrocarbons by far dominated the WSF (Table 1) and composed 99.1% of the total hydrocarbons measured. The remaining aromatic hydrocarbons, mostly the naphthalenes, were present at concentrations 100 times less than that of the monoaromatics. The hydrocarbons partitioned into the WSF from the crude oil in proportion to their solubility in seawater (Clark and MacLeod 1977; Bean et al. 1978).

TABLE 1.—Composition of the water soluble fraction of Prudhoe Bay crude oil. Sample size was 3 for the di- and triaromatics and 6 for the monoaromatics.

Fraction	mg/liter
Total alkanes	< 0.001
Naphthalene	.0851 ± 0.0088
Total methylnaphthalenes	.0766 ± 0.0080
Total dimethylnaphthalenes	.0269 ± 0.0015
Phenanthrene	.0006 ± 0.0004
Methylphenanthrene	< .0001
Dimethylphenanthrene	< .0001
Total polynuclear aromatics	.1892 ± 0.0175
Benzene	10.00 ± 0.29
Toluene	6.74 ± 0.42
Ethylbenzene	.30 ± 0.02
m- plus *p*-Xylene	1.12 ± 0.06
o-Xylene	1.12 ± 0.08
Total trimethyl benzenes	.46 ± 0.12
Total monoaromatics	19.75 ± 0.86
Total hydrocarbons measured	19.94

Detection Thresholds

Whereas Dungeness crabs detected both naphthalene and the WSF of Prudhoe Bay crude oil, the crabs detected the complex WSF mixture more readily and consistently. Because the percentage of crabs detecting naphthalene varied widely over

the range of concentrations presented, the regression equation relating percentage detection and the logarithm of concentration was not significant ($F = 1.3$, $P = 0.30$) (Figure 1). The curve for naphthalene detection was sawtooth-shaped with only four concentrations where the percentages of crabs detecting were above the upper 90% confidence limit about the control value. The sawtooth curve produced three concentrations at which 50% of the crabs could have detected naphthalene, 10^{-2}, 10^{-7}, and 10^{-9} mg/l. Because the factors producing the sawtooth curve are unknown, the most conservative approach is to consider the uppermost concentration, 10^{-2} mg/l, as the threshold for naphthalene detection. In contrast to naphthalene, the percentage of crabs detecting the WSF decreased in a consistent way with the WSF concentration (Figure 1). The regression equation was significant ($F = 60.4$, $P << 0.01$), and the variability was low ($R^2 = 91.0\%$). The 50% detection threshold from the regression equation was 4×10^{-4} mg/l, about 100 times lower than that for naphthalene.

When a crab detected naphthalene or WSF, the response was usually distinct. For crabs meeting the detection criteria, the median ratios of the antennular flicking rates did not vary with concentration (Median Tests, $\chi^2 = 2.38$, $P = 0.12$ for naphthalene; $\chi^2 = 9.07$, $P = 0.75$ for WSF), so that what varied with concentration was the percentage of crabs responding and not the magnitude of the response. Also, the magnitudes of the increase in antennular flicking were the same for both naphthalene and WSF. For naphthalene, the grand median of the antennular flicking rate ratios was 2.04; for the WSF, the grand median was 1.96.

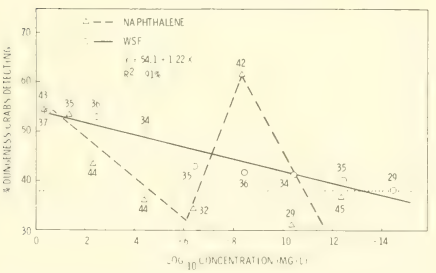


FIGURE 1.—Percentage of Dungeness crabs detecting naphthalene and the water soluble fraction (WSF) of crude oil as a function of the logarithm of concentration (mg/l). The percentage of crabs detecting a control of membrane-filtered seawater was 28.8% ($n = 66$) for naphthalene and 26.8% ($n = 41$) for WSF. The horizontal dotted line is the 90% confidence limit for the control values for both naphthalene and WSF (38%). The number beside each point is the number of trials at the concentration.

Discussion

When presented with naphthalene or WSF of crude oil, Dungeness crabs changed antennular orientation and flicking rate in the same manner as when presented with a clam extract. The blue crab also gives the same detection behaviors for hydrocarbons as for food (Pearson and Olla 1977, 1979, 1980; Pearson et al. in press). The similar findings in both species indicate that chemoreception by these crustaceans is not restricted to chemical cues for food and, thus, agree with Ache's (1975) suggestion that the chemical spectrum sensed by decapod crustaceans is really quite broad.

While the manner of antennular response to naphthalene and WSF was the same as that to a clam extract, the magnitudes of the flicking increase were slightly less and the chemosensory thresholds were 10^5 and 10^3 times higher than those found for the clam extract (Pearson et al. 1979). The grand median ratios of flicking rates for naphthalene and WSF, 2.04 and 1.96, were lower than that for the clam extract, 2.67. Also, the ranges of flicking ratios for the hydrocarbons were <30% of that for the clam extract. The slightly less intense response and much higher thresholds suggest that the petroleum hydrocarbons rank as much less potent chemical cues than sapid chemicals from a natural food.

Previously, Pearson and Olla (1980) had hypothesized that the chemical and chemosensory processes producing a higher detection threshold for a single petroleum hydrocarbon, naphthalene, than for a complex mixture of hydrocarbons, the WSF of crude oil, are analogous to the processes producing a similar relationship of thresholds for single amino acids and complex mixtures. Usually, food extracts and complex mixtures of amino acids and other chemicals have a lower detection threshold than that of a single amino acid (Mackie 1973; McLeese 1974). Indeed, with the Dungeness crab the detection threshold for WSF was about 100 times lower than that for naphthalene. Also, the variability in detection was much less for WSF than for naphthalene. This apparent greater dif-

ficulty in detecting the single hydrocarbon than the more complex WSF is presumptive evidence for the hypothesized analogy. With naphthalene constituting only 0.4% of the total hydrocarbons in the WSF, the crabs were probably responding primarily to other compounds or, perhaps, to some sort of odor medley.

One possible explanation for the extreme variability in naphthalene detection is that detection at high naphthalene concentrations was inhibited by some toxic, narcotic, or anesthetic action not present or much reduced at low concentrations. The blocking of chemosensory feeding and mating responses in the crab *Pachygrapsus crassipes* after 24-h exposure to naphthalene at 10^{-3} mg/l (Takahashi and Kittredge 1973) supports the possibility of such inhibition. If the threshold concentration for chemosensory inhibition was within the range of concentrations we presented, then a sharp increase in the percentage of crabs detecting naphthalene would be expected below the inhibition threshold and would produce the sawtooth-shaped curve seen for naphthalene in Figure 1. A sawtooth-shaped curve would also result if the sensitive antennular chemoreceptors were more impaired than the less sensitive body chemoreceptors on the dactyls, chelae, and mouthparts. If the antennular chemoreceptors were the more impaired at high naphthalene concentrations, detection would occur primarily through body chemoreceptors, and the antennular flicking increases would then derive from a reflex primarily involving the body chemoreceptors rather than one involving the antennular chemoreceptors. If the supposed chemosensory inhibition lessened or disappeared at low naphthalene levels, detection would switch to the more sensitive antennular chemoreceptors from the less sensitive body chemoreceptors. Whatever the explanation, the weak and inconsistent detection of naphthalene did not allow estimation of a threshold concentration by the method used here for WSF and elsewhere for food extracts (Pearson and Olla 1977; Pearson et al. 1979). Without more evidence concerning the mechanisms producing the particular shape of the naphthalene curve, the use of the apparently real peak in detection at 10^{-8} mg/l for estimating thresholds remains an open question. The most conservative approach for now is to consider 10^{-2} mg/l to be the naphthalene detection threshold.

For both food extract and petroleum hydrocarbons, the blue crab has exhibited more acute chemoreception than the Dungeness crab (Pearson and Olla 1977, 1979, 1980; Pearson et al. in press). Pearson et al. (1979) hypothesized that the lower detection threshold for clam extract seen in the blue crab was a consequence of the blue crab's greater ability to sample the chemical environment with its higher flicking rate and larger antennules. This hypothesis would apply equally to the differences between the two crabs in the hydrocarbon detection thresholds.

An important practical question is how the ability of the Dungeness crab to detect petroleum hydrocarbons compares with the range of hydrocarbon concentrations likely to be encountered by the crab. In the water column during an oil spill, McAuliffe et al. (1975) found concentrations of dissolved hydrocarbons ranging from 2×10^{-3} to 2×10^{-1} mg/l. Of these dissolved hydrocarbons about one-half were the monoaromatics dominating the WSF used here. During a spill from a North Sea platform, Grahl-Nielsen (1978) found petroleum hydrocarbon concentrations ranging up to 4×10^{-1} mg/l. In the open sea between Nova Scotia and Bermuda, Gordon et al. (1974) found petroleum hydrocarbon concentrations of 2.04×10^{-2}, 8×10^{-4}, and 4×10^{-4} mg/l at the surface, 1 m, and 5 m. These concentrations roughly agree with those given for relatively uncontaminated oceanic areas by Clark and MacLeod (1977), who also stated that chronically contaminated areas have hydrocarbon concentrations about two orders of magnitude higher than those of the open sea. Unfortunately, analytical difficulties in distinguishing petrogenic from biogenic hydrocarbons at low environmental concentrations make estimates of oil levels in chronically contaminated areas uncertain. For the North Sea, Grahl-Nielsen et al. (1979) found that despite considerable oil production there was no apparent standing crop of petroleum hydrocarbons, but rather petroleum contamination occurred as localized, transient patches. Thus, the petroleum hydrocarbon concentrations in uncontaminated (10^{-4} to 10^{-3} mg/l), chronically contaminated (10^{-4} to 10^{-2} mg/l), and oil spill (10^{-3} to 10^{-1} mg/l) situations are all at or above the WSF detection threshold (10^{-4} mg/l) so that Dungeness crabs can detect hydrocarbons readily at the concentrations found in oil spill situations, probably in chronically contaminated situations, and marginally in uncontaminated situations. In being able to detect the petroleum hydrocarbons at concentrations at and below those found in oil spill situations, Dungeness crabs can

achieve the first step to any subsequent behavioral response to petroleum.

Acknowledgments

We thank J. W. Anderson for his valuable discussions with us. The work was supported by the National Oceanic and Atmospheric Administration of the U.S. Department of Commerce under the Interagency Energy-Environment Program of the U.S. Environmental Protection Agency.

Literature Cited

ACHE, B. W.
1975. Antennular mediated host location by symbiotic crustaceans. Mar. Behav. Physiol. 3:125-130.

ANDERSON, J. W., J. M. NEFF, B. A. COX, H. E. TATUM, AND G. M. HIGHTOWER.
1974. Characteristics of dispersions and water-soluble extracts of crude and refined oils and their toxicity to estuarine crustaceans and fish. Mar. Biol. (Berl.) 27:75-88.

BEAN, R. M., J. W. BLAYLOCK, AND R. G. RILEY.
1978. Application of trace analytical techniques to the study of hydrocarbon composition upon dispersion of petroleum in a flowing seawater system. *In* Proceedings of a symposium on analytic chemistry of petroleum hydrocarbons in the marine aquatic environment, p. 902-908. Div. Pet. Chem., Am. Chem. Soc.

CLARK, R. C., JR., AND W. D. MACLEOD, JR.
1977. Inputs, transport mechanisms, and observed concentrations of petroleum in the marine environment. *In* D. C. Malins (editor), Effects of petroleum on arctic and subarctic marine environments and organisms. Vol I. Nature and fate of petroleum, p. 91-223. Acad. Press, N.Y.

FUZESSERY, Z. M.
1978. Quantitative stimulation of antennular chemoreceptors of the spiny lobster, *Panulirus argus*. Comp. Biochem. Physiol. 60A:303-308.

GORDON, D. C., JR., P. D. KEIZER, AND J. DALE.
1974. Estimates using fluorescence spectroscopy of the present state of petroleum hydrocarbon contamination in the water column of the northwest Atlantic Ocean. Mar. Chem. 2:251-261.

GRAHL-NIELSEN, O.
1978. The Ekofisk-Bravo blowout: petroleum hydrocarbons in the sea. *In* Proceedings of the conference on assessment of ecological impacts of oil spills, p. 476-487. Am. Inst. Biol. Sci., Arlington, Va.

GRAHL-NIELSEN, O., K. WESTRHEIM, AND S. WILHELMSEN.
1979. Petroleum hydrocarbons in the North Sea. *In* 1979 Oil spill conference, p. 629-632. Am. Pet. Inst., Wash., D.C.

HAZLETT, B. A.
1971. Antennule chemosensitivity in marine decapod Crustacea. J. Anim. Morph. Physiol. 18:1-10.

MACKIE, A. M.
1973. The chemical basis of food detection in the lobster, *Homarus gammarus*. Mar. Biol. (Berl.) 21:103-108.

MCAULIFFE, C. D.
1971. GC determination of solvents by multiple phase equilibration. Chem. Technol. 1:46-51.

MCAULIFFE, C. D., A. E. SMALLEY, R. D. GROOVER, W. M. WELSH, W. S. PICKLE, AND G. E. JONES.
1975. Chevron Main Pass Block 42 oil spill: chemical and biological investigations. *In* Proceedings of the 1975 joint conference on prevention and control of oil spills, p. 555-566. Am. Pet. Inst., Wash., D.C.

MCLEESE, D. W.
1974. Olfactory responses of lobsters (*Homarus americanus*) to solutions from prey species and to seawater extracts and chemical fractions of fish muscle and effects of antennule ablation. Mar. Behav. Physiol. 2:237-249.

OLLA, B. L., W. H. PEARSON, AND A. L. STUDHOLME.
1980. Applicability of behavioral measures in environmental stress assessment. *In* A. D. McIntyre and J. B. Pearce (editors), Biological effects of marine pollution and the problems of monitoring. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 179:162-173.

PEARSON, W. H., AND B. L. OLLA.
1977. Chemoreception in the blue crab, *Callinectes sapidus*. Biol. Bull. (Woods Hole) 153:346-354.
1979. Detection of naphthalene by the blue crab, *Callinectes sapidus*. Estuaries 2:64-65.
1980. Threshold for detection of naphthalene and other behavioral responses by the blue crab, *Callinectes sapidus*. Estuaries 3:224-229.

PEARSON, W. H., S. E. MILLER, J. W. BLAYLOCK, AND B. L. OLLA.
In press. Detection of the water-soluble fraction of crude oil by the blue crab, *Callinectes sapidus*. Mar. Environ. Res.

PEARSON, W. H., P. C. SUGARMAN, D. L. WOODRUFF, AND B. L. OLLA.
1979. Thresholds for detection and feeding behavior in the Dungeness crab, *Cancer magister* (Dana). J. Exp. Mar. Biol. Ecol. 39:65-78.

TAKAHASHI, F. T., AND J. S. KITTREDGE.
1973. Sublethal effects of the water soluble component of oil: Chemical communication in the marine environment. *In* D. G. Ahearn and S. P. Meyers (editors), The microbial degradation of oil pollutants, p. 259-264. La. State Univ. Press Publ. LSU-SG-73-01.

WALTER H. PEARSON
PETER C. SUGARMAN
DANA L. WOODRUFF
J. W. BLAYLOCK

Battelle, Pacific Northwest Laboratories
Marine Research Laboratory
358B Washington Harbor Road
Sequim, WA 98382

BORI L. OLLA

Northeast Fisheries Center Sandy Hook Laboratory
National Marine Fisheries Service, NOAA
Highlands, NJ 07732

NOTICES

NOAA Technical Reports NMFS published during first 6 months of 1980.

Circular

430. Guide to identification of some sculpin (Cottidae) larvae from marine and brackish waters off Oregon and adjacent areas in the northeast Pacific. By Sally L. Richardson and Betsy B. Washington. January 1980, iv + 56 p., 32 fig., 45 tables. For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402 - Stock No. 003-017-00472-4.

431. Guide to some trawl-caught marine fishes from Maine to Cape Hatteras, North Carolina. By Donald D. Flescher. March 1980, iii + 34 p., [137 fig.]. For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402.

432. Synopsis of biological data on bonitos of the genus *Sarda*. By Howard O. Yoshida. May 1980, iv + 50 p., 43 fig., 26 tables. Also FAO Fisheries Synopsis No. 118.

433. Synopsis of biological data on striped bass, *Morone saxatilis* (Walbaum). By Eileen M. Setzler, Walter R. Boynton, Kathryn V. Wood, Henry H. Zion, Lawrence Lubbers, Nancy K. Mountford, Phyllis Frere, Luther Tucker, and Joseph A. Mihursky. June 1980, v + 69 p., 9 fig., 24 tables. Also FAO Fisheries Synopsis No. 121.

Special Scientific Report — Fisheries

740. Food of fifteen northwest Atlantic gadiform fishes. By Richard W. Langton and Ray E. Bowman. February 1980, iv + 23 p., 3 fig., 11 tables.

Most NOAA publications are available by purchase from the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402. Individual copies of NOAA Technical Reports (in limited numbers) are available free to Federal and State government agencies and may be obtained by writing to User Services Branch (D822), Environmental Science Information Center, NOAA, Rockville, MD 20852.

INFORMATION FOR CONTRIBUTORS TO THE *FISHERY BULLETIN*

Manuscripts submitted to the *Fishery Bulletin* will reach print faster if they conform to the following instructions. These are not absolute requirements, of course, but desiderata.

CONTENT OF MANUSCRIPT

The **title page** should give only the title of the paper, the author's name, his affiliation, and mailing address, including ZIP code.

The **abstract** should not exceed one double-spaced page.

In the **text,** *Fishery Bulletin* style, for the most part, follows that of the *U.S. Government Printing Office Style Manual.* Fish names follow the style of the American Fisheries Society Special Publication No. 6, *A List of Common and Scientific Names of Fishes from the United States and Canada,* Third Edition, 1970.

Text footnotes should be typed separately from the text.

Figures and **tables,** with their legends and headings, should be self-explanatory, not requiring reference to the text. Their placement should be indicated in the right-hand margin of the manuscript.

Preferably **figures** should be reduced by photography to 5¾ inches (for single-column figures, allowing for 50% reduction in printing), or to 12 inches (for double-column figures). The maximum height, for either width, is 14 inches. Photographs should be printed on glossy paper.

Do not send original drawings to the Scientific Editor; if they, rather than the photographic reductions, are needed by the printer, the Scientific Publications Office will request them.

Each **table** should start on a separate page. Consistency in headings and format is desirable. Vertical rules should be avoided, as they make the tables more expensive to print. Footnotes in tables should be numbered sequentially in arabic numerals. To avoid confusion with powers, they should be placed to the *left* of numerals.

Acknowledgments, if included, are placed at the end of the text.

Literature is cited in the text as: Lynn and Reid (1968) or (Lynn and Reid 1968). All papers referred to in the text should be listed alphabetically by the senior author's surname under the heading "Literature Cited." Only the author's surname and initials are required in the **literature cited.** The accuracy of the **literature cited** is the responsibility of the author. Abbreviations of names of periodicals and serials should conform to *Biological Abstracts List of Serials with Title Abbreviations. (Chemical Abstracts* also uses this system, which was developed by the American Standards Association.)

Common **abbreviations** and **symbols,** such as mm, m, g, ml, mg, ° C (for Celsius), %, ‰ and so forth, should be used. Abbreviate units of measure only when used with numerals. Periods are only rarely used with abbreviations.

We prefer that **measurements** be given in metric units; other equivalent units may be given in parentheses.

FORM OF THE MANUSCRIPT

The original of the manuscript should be typed, double-spaced, on white bond paper. Please triple space above headings. We would rather receive good duplicated copies of manuscripts than carbon copies. The sequence of the material should be:

TITLE PAGE
ABSTRACT
TEXT
LITERATURE CITED
APPENDIX
TEXT FOOTNOTES
TABLES (Each table should be numbered with an arabic numeral and heading provided)
LIST OF FIGURES (Entire figure legends)
FIGURES (Each figure should be numbered with an arabic numeral; legends are desired)

ADDITIONAL INFORMATION

Send the ribbon copy and two duplicated or carbon copies of the manuscript to:

Dr. Carl J. Sindermann, Scientific Editor
Fishery Bulletin
Northeast Fisheries Center
Sandy Hook Laboratory
National Marine Fisheries Service, NOAA
Highlands, NJ 07732

Fifty **separates** will be supplied to an author free of charge and 100 supplied to his organization. No covers will be supplied.

Contents–continued

FOGARTY, MICHAEL J., DAVID V. D. BORDEN, and HOWARD J. RUSSELL. Movements of tagged American lobster, *Homarus americanus*, off Rhode Island ... 771
RENSEL, JOHN E., and EARL F. PRENTICE. Factors controlling growth and survival of cultured spot prawn, *Pandalus platyceros*, in Puget Sound, Washington 781

Notes

THEILACKER, GAIL H. Rearing container size affects morphology and nutritional condition of larval jack mackerel, *Trachurus symmetricus* 789
CARNEY, ROBERT S., and ANDREW G. CAREY, JR. Effectiveness of metering wheels for measurement of area sampled by beam trawls 791
PITCHER, KENNETH W. Stomach contents and feces as indicators of harbor seal, *Phoca vitulina*, foods in the Gulf of Alaska 797
CHRISTENSEN, DARRYL J., and WALTER J. CLIFFORD. The 1978 spring recreational catch of Atlantic mackerel, *Scomber scombrus*, off the Middle Atlantic region 799
BEARDSLEY, GRANT L. Size and possible origin of sailfish, *Istiophorus platypterus*, from the eastern Atlantic Ocean 805
RICE, STANLEY D., and JACK E. BAILEY. Ammonia concentrations in pink salmon, *Oncorhynchus gorbuscha*, redds of Sashin Creek, southeastern Alaska ... 809
HUNTER, JOHN R., and CAROL A. KIMBRELL. Egg cannibalism in the northern anchovy, *Engraulis mordax* 811
QUINN, THOMAS P., BRUCE S. MILLER, and R. CRAIG WINGERT. Depth distribution and seasonal and diel movements of ratfish, *Hydrolagus colliei*, in Puget Sound, Washington 816
PEARSON, WALTER H., PETER C. SUGARMAN, DANA L. WOODRUFF, J. W. BLAYLOCK, and BORI L. OLLA. Detection of petroleum hydrocarbons by the Dungeness crab, *Cancer magister* 821

Notices

NOAA Technical Reports NMFS published during the first 6 months of 1980 827

☆ GPO 696-404

Fishery Bulletin

Vol. 78, No. 4 October 1980

BRAY, RICHARD N. Influence of water currents and zooplankton densities on daily foraging movements of blacksmith, *Chromis punctipinnis*, a planktivorous reef fish 829

BREIWICK, JEFFREY M., EDWARD D. MITCHELL, and DOUGLAS G. CHAPMAN. Estimated initial population size of the Bering Sea stock of bowhead whale, *Balaena mysticetus*: an iterative method 843

RICHARDSON, SALLY L. Spawning biomass and early life of northern anchovy, *Engraulis mordax*, in the northern subpopulation off Oregon and Washington ... 855

DURBIN, ANN G., EDWARD G. DURBIN, PETER G. VERITY, and THOMAS J. SMAYDA. Voluntary swimming speeds and respiration rates of a filter-feeding planktivore, the Atlantic menhaden, *Brevoortia tyrannus* (Pisces: Clupeidae) 877

MENDELSSOHN, ROY. Using Box-Jenkins models to forecast fishery dynamics: identification, estimation, and checking 887

LAROCHE, WAYNE A. Development of larval smooth flounder, *Liopsetta putnami*, with a redescription of development of winter flounder, *Pseudopleuronectes americanus* (family Pleuronectidae) 897

MODDE, TIMOTHY, and STEPHEN T. ROSS. Seasonality of fishes occupying a surf zone habitat in the northern Gulf of Mexico 911

MATARESE, ANN C., SALLY L. RICHARDSON, and JEAN R. DUNN. Larval development of Pacific tomcod, *Microgadus proximus*, in the northeast Pacific Ocean with comparative notes on larvae of walleye pollock, *Theragra chalcogramma*, and Pacific cod, *Gadus macrocephalus* (Gadidae) 923

Notes

AINLEY, DAVID G., CRAIG S. STRONG, HARRIET R. HUBER, T. JAMES LEWIS, and STEPHEN H. MORRELL. Predation by sharks on pinnipeds at the Farallon Islands 941

GRISWOLD, CAROLYN A., and JEROME PREZIOSO. In situ observations on reproductive behavior of the long-finned squid, *Loligo pealei* 945

LEWIS, ROBERT M., and CHARLES M. ROITHMAYR. Spawning and sexual maturity of Gulf menhaden, *Brevoortia patronus* 947

(Continued on next page)

Seattle, Washington

U.S. DEPARTMENT OF COMMERCE

Malcolm Baldrige, *Secretary*

NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION

Terry L. Leitzell, *Assistant Administrator for Fisheries*

NATIONAL MARINE FISHERIES SERVICE

Fishery Bulletin

The *Fishery Bulletin* carries original research reports and technical notes on investigations in fishery science, engineering, and economics. The Bulletin of the United States Fish Commission was begun in 1881; it became the Bulletin of the Bureau of Fisheries in 1904 and the Fishery Bulletin of the Fish and Wildlife Service in 1941. Separates were issued as documents through volume 46; the last document was No. 1103. Beginning with volume 47 in 1931 and continuing through volume 62 in 1963, each separate appeared as a numbered bulletin. A new system began in 1963 with volume 63 in which papers are bound together in a single issue of the bulletin instead of being issued individually. Beginning with volume 70, number 1, January 1972, the *Fishery Bulletin* became a periodical, issued quarterly. In this form, it is available by subscription from the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402. It is also available free in limited numbers to libraries, research institutions, State and Federal agencies, and in exchange for other scientific publications.

EDITOR

Dr. Jay C. Quast
Scientific Editor, *Fishery Bulletin*
Northwest and Alaska Fisheries Center
Auke Bay Laboratory
National Marine Fisheries Service, NOAA
P.O. Box 155, Auke Bay, AK 99821

Editorial Committee

Dr. Bruce B. Collette
National Marine Fisheries Service

Dr. Edward D. Houde
Chesapeake Biological Laboratory

Dr. Merton C. Ingham
National Marine Fisheries Service

Dr. Reuben Lasker
National Marine Fisheries Service

Dr. Jerome J. Pella
National Marine Fisheries Service

Dr. Sally L. Richardson
Gulf Coast Research Laboratory

Kiyoshi G. Fukano, Managing Editor

The *Fishery Bulletin* (USPS 090-870) is published quarterly by Scientific Publications Office, National Marine Fisheries Service, NOAA, Room 336, 1700 Westlake Avenue North, Seattle, WA 98109. Controlled circulation paid to Finance Department, USPS, Washington, DC 20260.

Although the contents have not been copyrighted and may be reprinted entirely, reference to source is appreciated.

The Secretary of Commerce has determined that the publication of this periodical is necessary in the transaction of the public business required by law of this Department. Use of funds for printing of this periodical has been approved by the Director of the Office of Management and Budget through 31 March 1982.

Fishery Bulletin

CONTENTS

Vol. 78, No. 4 October 1980

BRAY, RICHARD N. Influence of water currents and zooplankton densities on daily foraging movements of blacksmith, *Chromis punctipinnis*, a planktivorous reef fish 829

BREIWICK, JEFFREY M., EDWARD D. MITCHELL, and DOUGLAS G. CHAPMAN. Estimated initial population size of the Bering Sea stock of bowhead whale, *Balaena mysticetus*: an iterative method 843

RICHARDSON, SALLY L. Spawning biomass and early life of northern anchovy, *Engraulis mordax*, in the northern subpopulation off Oregon and Washington ... 855

DURBIN, ANN G., EDWARD G. DURBIN, PETER G. VERITY, and THOMAS J. SMAYDA. Voluntary swimming speeds and respiration rates of a filter-feeding planktivore, the Atlantic menhaden, *Brevoortia tyrannus* (Pisces: Clupeidae) 877

MENDELSSOHN, ROY. Using Box-Jenkins models to forecast fishery dynamics: identification, estimation, and checking 887

LAROCHE, WAYNE A. Development of larval smooth flounder, *Liopsetta putnami*, with a redescription of development of winter flounder, *Pseudopleuronectes americanus* (family Pleuronectidae) 897

MODDE, TIMOTHY, and STEPHEN T. ROSS. Seasonality of fishes occupying a surf zone habitat in the northern Gulf of Mexico 911

MATARESE, ANN C., SALLY L. RICHARDSON, and JEAN R. DUNN. Larval development of Pacific tomcod, *Microgadus proximus*, in the northeast Pacific Ocean with comparative notes on larvae of walleye pollock, *Theragra chalcogramma*, and Pacific cod, *Gadus macrocephalus* (Gadidae) 923

Notes

AINLEY, DAVID G., CRAIG S. STRONG, HARRIET R. HUBER, T. JAMES LEWIS, and STEPHEN H. MORRELL. Predation by sharks on pinnipeds at the Farallon Islands 941

GRISWOLD, CAROLYN A., and JEROME PREZIOSO. In situ observations on reproductive behavior of the long-finned squid, *Loligo pealei* 945

LEWIS, ROBERT M., and CHARLES M. ROITHMAYR. Spawning and sexual maturity of Gulf menhaden, *Brevoortia patronus* 947

(Continued on next page)

Seattle, Washington

1981

For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402—Subscription price per year: $14.00 domestic and $17.50 foreign. Cost per single issue: $4.00 domestic and $5.00 foreign.

STROUD, RICHARD K., CLIFFORD H. FISCUS, and HIROSHI KAJIMURA. Food of the Pacific white-sided dolphin, *Lagenorhynchus obliquidens*, Dall's porpoise, *Phocoenoides dalli*, and northern fur seal, *Callorhinus ursinus*, off California and Washington 951
MARLIAVE, JEFFREY B. Spawn and larvae of the Pacific sandfish, *Trichodon trichodon* 959
McCLELLAN, G. L., and J. K. LEONG. A radiologic method for examination of the gastrointestinal tract in the Atlantic ridley, *Lepidochelys kempi*, and loggerhead, *Caretta caretta*, marine turtles 965
CLAUSEN, DAVID M. Summer food of Pacific cod, *Gadus macrocephalus*, in coastal waters of southeastern Alaska 968
KHILNANI, ARVIND. Use of Griffin's yield model for the Gulf of Mexico shrimp fishery 973
GOLDBERG, STEPHEN R. Seasonal spawning cycle of the Pacific butterfish, *Peprilus simillimus* (Stromateidae) 977
DAVIS, GARY E. Effects of injuries on spiny lobster, *Panulirus argus*, and implications for fishery management 979

INDEX, VOLUME 78 985

Vol. 78, No. 3 was published on 11 February 1981.

The National Marine Fisheries Service (NMFS) does not approve, recommend or endorse any proprietary product or proprietary material mentioned in this publication. No reference shall be made to NMFS, or to this publication furnished by NMFS, in any advertising or sales promotion which would indicate or imply that NMFS approves, recommends or endorses any proprietary product or proprietary material mentioned herein, or which has as its purpose an intent to cause directly or indirectly the advertised product to be used or purchased because of this NMFS publication.

INFLUENCE OF WATER CURRENTS AND ZOOPLANKTON DENSITIES ON DAILY FORAGING MOVEMENTS OF BLACKSMITH, *CHROMIS PUNCTIPINNIS*, A PLANKTIVOROUS REEF FISH

RICHARD N. BRAY[1]

ABSTRACT

The blacksmith, *Chromis punctipinnis*, one of the most abundant fishes in kelp forests off southern California, daily emerges from rock shelters and moves to specific locations where it forages in the midwater on zooplankton. Midwater transects taken over a reef that experiences occasional reversals in water currents indicated that large blacksmith (greater than 150 mm total length) consistently gathered at the incurrent end of the reef. These movements are probably related to the availability of food. Replicate plankton tows taken near the ends of the reef demonstrated that zooplankton densities were greater at the incurrent end. Experiments in which large fish were placed in cages suspended in midwater at both reef ends demonstrated that individuals foraging at the incurrent end consumed more prey. Small blacksmith (less than 125 mm total length) did not undergo foraging movements. Instead, most remained in the shallower portions of the reef, close to cover, even though caging experiments and collections of free-living individuals indicated that these fish would consume more prey if they moved upcurrent. Since small as well as large blacksmith benefit from foraging at the incurrent end, the size-specific differences in foraging movements probably reflect differences in the cost of migrating in terms of time, energy, and predation.

Many fishes on temperate and tropical reefs feed heavily on zooplankton. They eat either by day or by night, and school or shelter when inactive (Hobson 1972, 1973, 1974; Hobson and Chess 1976). Some planktivores limit their movements to the water column above their shelters (e.g., Sale 1971; Hobson 1972, 1973); the distribution and small-scale movements of these parochial species have been the subject of recent quantitative investigations (e.g., Stevenson 1972; Hobson and Chess 1978; de Boer 1978). Other planktivores undergo extensive horizontal movements (Hobson 1972, 1973), and have received less attention. Nonetheless, migrating planktivores are often extremely abundant and probably import substantial amounts of extrinsic energy—drift zooplankton—into reef communities (Stevenson 1972).

The blacksmith, *Chromis punctipinnis*, a planktivorous pomacentrid that may grow to a total length (TL) of 300 mm (Miller and Lea 1972), is one of the most abundant fishes inhabiting the inshore rocky reefs of southern California. In aggregations of up to several hundred individuals, they feed throughout the day on a variety of zooplankton, including larvaceans, copepods, cladocerans, and various larvae (Hobson and Chess 1976). At dusk, they descend to the reef surface where they shelter in holes and crevices until dawn (Ebeling and Bray 1976; Hobson and Chess 1976). Many tropical congeners of the blacksmith have similar activity patterns (e.g., Hobson 1965, 1972; Collette and Talbot 1972; Emery 1973).

During preliminary observations on rocky reefs near Santa Barbara, Calif., I found that blacksmith often forage and shelter in different areas. Large numbers of blacksmith emerge from shelters at dawn, assemble into a school, and move to a location above a reef, where they disperse into a loose aggregation in the midwater and forage on zooplankton. At least some blacksmith near Santa Catalina Island, Calif., show a similar pattern (Hobson and Chess 1976). In commenting on the location of daytime foraging aggregations, Limbaugh (1955) observed that, "Thick schools of young to half-grown blacksmith often form where a plankton-rich current enters the kelp bed." Such a response to water currents would enable blacksmith to be among the first of many vertebrate and invertebrate planktivores to forage on plankton as it is swept across the reef community. However,

[1] Department of Biological Sciences, University of California, Santa Barbara, Calif.; present address: Department of Biology, California State University, Long Beach, CA 90840.

Manuscript accepted March 1980.
FISHERY BULLETIN: VOL. 78, NO. 4, 1981.

other factors may also affect the distribution of blacksmith. For example, kelp and high relief rocks may serve as orientation points or shelter for fish in the water column (Limbaugh 1955; Quast 1968a, b, c; Ebeling and Bray 1976; Hobson and Chess 1976).

In this paper, I first examine the distribution of blacksmith in relation to water currents over a reef that is subjected to occasional reversals in current flow to see if they consistently gather at the incurrent end. Since foraging is the major activity of blacksmith while assembled in these midwater aggregations, I then determine if plankton is more abundant at the incurrent end. Finally, by examining caged and free-living individuals, I see whether blacksmith that forage at the incurrent end consume more prey.

METHODS

Study Site

Naples Reef is a large rocky outcrop (275 × 80 m) located 24 km west of Santa Barbara and 1.6 km offshore (Figure 1). The substratum is a series of uplifted sandstone rills and ridges that parallel the coast. Depths across the reef average 8-10 m, although some prominences come to within 5 m of the surface. A sandy bottom 16-20 m deep surrounds the reef, with rocky outcrops inshore and cobbles offshore. The assemblage of plant and animal life on and around the reef is among the richest along the Santa Barbara coast. Giant kelp, *Macrocystis pyrifera*, is always present on the reef, although kelp densities fluctuated considerably throughout the study period. The species composition and abundance of fishes at Naples Reef are listed in Ebeling et al. (1980).

Naples Reef is well suited to study the effects of water currents on the distribution of fish. The reef is almost always swept by measurable longshore currents. Although usually these come from the east, occasionally they come from the west. A shift in the distribution of fish when the currents reverse would provide strong evidence that water currents affect the fish's distribution.

Surveys

In December 1975, I initiated biweekly counts of all fish in the water column at four sites on the reef (Figure 1). At each site, I fixed a line from a

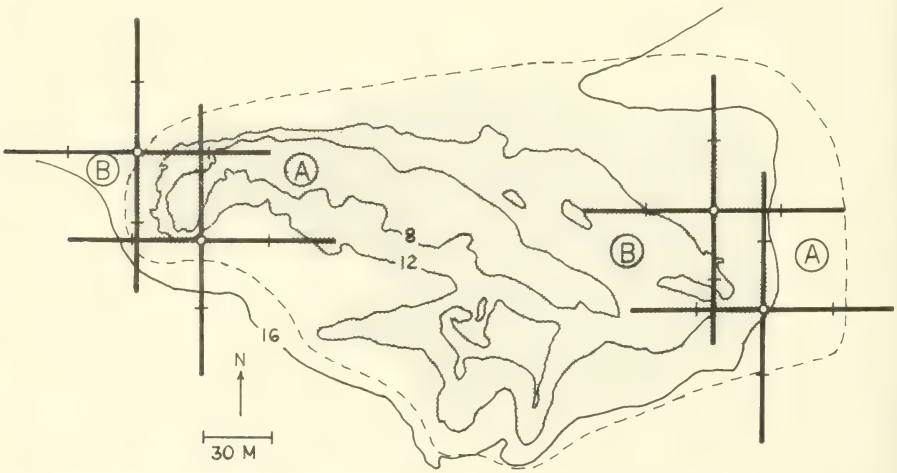


FIGURE 1.—Contour map of Naples Reef, southern California. Heavy lines indicate locations of midwater transects: 30 m (to cross mark) and 60 m (to end) from the starting points (circles). Letters indicate incurrent and excurrent locations where zooplankton were sampled: A locations—when current flowed from the east; B locations—when current flowed from the west. Midwater cages were located at the A locations. The shaded portion indicates the rocky substratum, while the surrounding open area represents sand. The dashed line indicates the margin of the kelp bed. Depths are in meters.

permanent anchoring point to a buoy within 1 m of the surface. At middepth (6 m), I attached a transect line and swam four transects at a constant speed, one each to the north, east, south, and west. Without moving my head, I counted all blacksmith within my field of view. Fish were tallied in separate columns on a slate according to their size as estimated by eye: juveniles (<125 mm TL), halfgrown fish (125-150 mm), and adults (>150 mm). These classes refer to sizes and not necessarily to stages of sexual maturity. A complete survey consisted of 16 transects: 4 at each of the four sites on the reef. During the first 26 surveys (9 December 1975-2 November 1976), the length of the transect line was 30 m, so a total of 480 m were traversed each survey. For the remaining 13 surveys (9 November 1976-23 July 1977), the length of the transects was doubled to 60 m each (960 m/survey) to see if large aggregations of blacksmith occurred beyond the areas that were initially sampled. I did not conduct surveys when visibility was <2 m.

I also examined several oceanographic variables at each site on the reef. Water visibility was measured during each transect as the distance at which I could easily discern a fishlike silhouette attached to the line. Water velocities were measured several times at each site by timing the movement of small particles. And surface, midwater, and bottom water temperatures were taken with a small dial thermometer.

Plankton Sampling

Once the movements of blacksmith were determined, I made replicate zooplankton tows at known sheltering sites near the excurrent end of the reef, and known foraging sites at the incurrent end. Incurrent samples were collected at the margin of the kelp bed, over the sand bottom that surrounds the reef. Excurrent samples were taken within the bed, above rocky areas that provide shelter for large numbers of blacksmith at night. The exact location of the sample sites depended on the direction of the water currents (Figure 1). I specifically avoided sampling on days when the current velocity was negligible, when there were obvious eddies, or when the current flow was not along the east-west axis of the reef.

Plankton were collected between 1000 and 1400 h with a 0.5 m diameter 0.333 mm mesh net pushed by a diver. A TSK[2] flowmeter, fitted across the net opening, measured the filtered volume of water. I randomized (by coin flip) my choice of which end to sample first, thereby restricting such variables as collection time, net clogging, diver fatigue, etc., to random error. Each tow was double oblique, going from the surface to a depth of 6 m, then back to the surface. The diver swam a haphazard pattern through the kelp bed and avoided sampling within 1 m of a kelp plant or the bottom. All samples were immediately fixed in 5% buffered Formalin. The time interval between the first and last tows in a collection ranged from 1.5 to 4.5 h.

In the laboratory, samples were split with a Folsum plankton splitter: one-half was used for weighing and the other half was used for counting. For dry weights, samples were filtered (vacuum pressure = 725 mm Hg) onto preweighed GF/C filters, and dried at 60° C to a constant weight. For counting, samples were split two more times, then subsampled with three 10 ml aliquots drawn with a Stemple pipette. The plankton were counted under a dissecting microscope and sorted into broad taxonomic categories. Weights and counts were standardized by conversion to amounts per cubic meter of water sampled.

I analyzed the data in two ways to compare densities of zooplankton between incurrent and excurrent ends of the reef. First, I compared the individual incurrent and excurrent samples within each collection by Mann-Whitney *U*-tests to look for significant differences in densities between the reef ends. Second, I compared mean densities between incurrent and excurrent samples of each collection, and tested for incurrent-excurrent differences in these means among the eight collections with Wilcoxon's signed-ranks tests; thus, each collection was a paired (incurrent versus excurrent) observation.

Foraging Experiments

To see if blacksmith near the incurrent end consume more prey, I compared gut contents of fish that foraged near the incurrent kelp margin and excurrent shelter sites. I did not compare free-living adults because they were relatively rare near the excurrent end and their major activity might not have been foraging. Instead, I placed individuals in cages located at both ends of the reef. Cages were constructed of a 1 × 1 × 1 m

[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

wooden frame covered with galvanized chicken wire, which allowed fairly free passage of water through the enclosure. For experiments using larger fish (>125 mm SL, standard length) the mesh measured 2.5 × 3.7 cm; mesh size was halved to 1.3 × 1.9 cm when smaller fish were used. Seine floats were attached to the top of the cages to make them positively buoyant, and the cages were suspended in midwater at a depth of 5 m by a length of rope anchored to the substratum. The cages were located in the same areas on the reef from which plankton were sampled. One cage was placed at the eastern margin of the kelp bed, 60 m east of the reef. The other was placed over the reef top, 50 m from the extreme west end of the reef (Figure 1). When half of the experiments were completed, the cages were translocated.

Blacksmith were captured while in shelters with the anesthetic quinaldine, or while attracted to chum stations (broken sea urchins). Fish were placed in holding tanks on the boat and haphazardly assigned to a cage. One to five fish were captured for each cage. Before each experiment, the cages were scrubbed with a brush to remove encrusting organisms. When fish were placed in the cage, they swam to the bottom; by the next day, they had usually gathered in the middle. At night, the fish nestled in the bottom corners of the cage.

Each experiment lasted 7-10 d. Preliminary experiments indicated that at least 5 d were required before caged fish began to feed. Fish were removed from cages in the midafternoon and fixed in buffered Formalin. On three occasions, I speared free-living fish in the vicinity of the incurrent cage at the same time that caged fish were removed, to see if caging affected the fish's diet. Since smaller blacksmith do not undergo large-scale movements and are abundant throughout the reef, I also compared gut contents of free-living juveniles speared at the incurrent and excurrent ends. For all collections, blacksmith at the incurrent end were removed first; those at the excurrent end within an hour later. Thus, positive differences in gut fullness between incurrent and excurrent fish are conservative because excurrent fish were able to forage for a longer period of time.

In the laboratory, fish were measured for standard length, blotted weight, and displaced volume. The gut was removed and divided into stomach and intestine. The contents of each were measured for displaced volume, then examined under a dissecting microscope and identified into broad taxonomic categories. Finally, contents were washed onto a preweighed filter and dried at 60° C to a constant weight.

To standardize for differences in fish sizes, the volumes and weights of the gut contents were expressed as relative measures: 1) volumetric fullness as $(Vg/Vf) \times 10^3$, where Vg is the displaced volume (in milliliters) of the gut contents, and Vf is the displaced volume (in milliliters) of the intact fish; 2) gravimetric fullness as: $(Wg/Wf) \times 10^4$, where Wg and Wf represent weights (in grams) of the gut contents and intact fish. Finally, for each experiment, I scaled volumetric and gravimetric fullness from 1.0 for the largest value, down toward 0, then averaged the two scaled values to obtain an overall estimate of gut fullness. This enabled me to pool data among experiments to increase sample size.

RESULTS

Physical Measurements

I made 39 surveys between December 1975 and July 1977. However, since water visibility directly influenced the volume of water in which I counted fish, I excluded from further analysis those surveys when mean visibility was significantly greater at the incurrent end of the reef (t-tests; $P<0.05$) or when variances in visibility at the incurrent and excurrent ends were heterogeneous (F-tests, $P<0.05$). In the remaining 27 surveys, water flowed over the reef from the east in 23; on 4 occasions (twice in April 1976, once in August 1976, and once in January 1977), the current was reversed and flowed from the west. Mean monthly water visibility ranged from 4.5 m in March to 8.7 m in December. Visibility was slightly greater at the excurrent end of the reef. When the current flowed from the east, visibility averaged 7.1 m at the east end and 7.4 m at the west end; when the current reversed, visibility averaged 6.0 m and 5.1 m at the east and west ends.

Spot checks on the movements of small particles indicated that the net flow of water was roughly unidirectional over most of the reef; this general flow was confirmed on 2 d when pieces of kelp were followed as they drifted the length of the reef (Bailey[3]). Nonetheless, variances in velocity were significantly heterogeneous between reef ends for

[3]Thomas Bailey, Marine Science Institute, University of California, Santa Barbara, CA 93106, pers. commun. June 1977.

individual measurements (F-max test, $P<0.001$), and for mean velocities among all 27 surveys (variances were: 41.10 incurrent, 16.05 excurrent; $P<0.05$). These variations were presumably caused by local turbulence produced by kelp and rocky prominences.

Current velocities were consistently greater at the incurrent reef end. When water flowed from the east, mean incurrent and excurrent velocities were 11.0 cm/s and 4.6 cm/s (Wilcoxon's signed-ranks test, $P<0.001$). When currents were reversed, incurrent and excurrent velocities were 4.9 and 3.6 cm/s ($P>0.25$); these differences probably would be significant with a larger sample size.

Water temperatures at the surface and midwater averaged 15.6° and 15.3° C, and both ranged from 13° C in April to 20° C in October. Bottom temperatures showed a similar pattern, but averaged approximately 2° C lower. Temperatures taken in 21 surveys when the current flowed from the east did not differ significantly between reef ends at any of the three depths (t-tests for paired samples, $P>0.25$). I recorded temperatures on only two of the four surveys when currents flowed from the west. Surface and midwater temperatures both averaged around 15° C while bottom temperatures averaged 13° C. I could not detect differences in temperatures between reef ends.

Role of Water Currents

The patterns in water visibility simplified my analysis of the fish counts. I treated each of the 27 surveys as a pair of samples, one from the incurrent and the other from the excurrent reef end. Each member of a pair consisted of a total count of blacksmith from the eight transects taken at one end of the reef (Figure 1). Differences within each pair were then analyzed among surveys with one-tailed nonparametric tests, with the hypothesis that counts of blacksmith are greater at the incurrent reef end. The similarity in water visibility between reef ends automatically standardized the counts for the volume of water that was sampled. Actually, the test of the hypothesis was conservative because visibility (hence the volume of water sampled) was significantly lower at the incurrent end in 6 of 27 surveys. I also calculated for each survey the proportion of blacksmith counted at each end of the reef. Proportions were arc sine transformed for computation of 95% confidence intervals (CI). I checked the precision of my surveys on two occasions by having another diver swim abreast of me and count blacksmith independently. Our total counts of adult blacksmith were similar: 103 (RNB) versus 112 (partner), and 254 (RNB) versus 273 (partner). Moreover, the surveys seemed to confirm our subjective impressions on the relative abundance of adult blacksmith and other fishes in the midwater.

Blacksmith were the most abundant fish in the midwater and were recorded on every survey. Other abundant fishes in the midwater were kelp bass, *Paralabrax clathratus*, and señorita, *Oxyjulis californica* (Table 1).

Adult blacksmith invariably aggregated at the incurrent end (Table 2). In each of the 27 surveys, more adults were counted at the incurrent than at the excurrent end (Wilcoxon's signed-ranks test, $P<0.001$). Doubling the length of transects had little effect on the counts of adults at the excurrent end, but resulted in a 3- to 4-fold increase in counts of adults at the incurrent end. This was because large numbers of adults gathered farther upcurrent, beyond the area covered in the short transects. The average proportion of adults at the east end of the reef was 0.99 (95% CI = 0.92-1.0) when it was the incurrent end, and 0.09 (95% CI = 0-0.32) when it was the excurrent end.

Adults respond quickly to changes in current direction. On one occasion around midday, the current reversed during a survey and the adults

TABLE 1.—Relative abundance (percentage of total individuals) and frequency of occurrence (percent of total surveys) of fishes counted in midwater transects at Naples Reef, southern California. Species are listed in order of decreasing abundance.

Species	Percentage of total individuals	Frequency (%)
Chromis punctipinnis	41.58	100.0
Paralabrax clathratus	22.04	100.0
Oxyjulis californica	9.47	81.5
Medialuna californiensis	9.00	92.6
Sebastes mystinus	8.62	55.6
Atherinops affinis	2.70	22.2
Trachurus symmetricus	1.82	25.9
Phanerodon furcatus	1.68	33.3
Sebastes serranoides	0.64	66.7
Brachyistius frenatus	0.59	33.3
Embiotoca jacksoni	0.42	33.3
Phanerodon atripes	0.39	18.5
Seriola dorsalis	0.29	11.1
Rhacochilus toxotes	0.21	18.5
Sebastes atrovirens	0.20	25.9
Embiotoca lateralis	0.20	3.7
Damalichthys vacca	0.05	22.2
Heterostichus rostratus	0.04	14.8
Girella nigricans	0.03	3.7
Mola mola	0.03	11.1
Torpedo californica	0.01	7.4
Sarda chiliensis	0.01	3.7
Total no. of individuals	7,767	
Total no. of surveys	27	

TABLE 2.—Number of blacksmith per survey, average (median), in midwater surveys at the east and west ends of Naples Reef, southern California. Freq. = frequency of occurrence (percent of surveys). Short transects total 480 m; long total 960 m.

Current direction	Length of transects	No. surveys	Adults			Halfgrowns			Juveniles		
			Freq. (%)	East	West	Freq. (%)	East	West	Freq. (%)	East	West
East to west	short	16	100.0	44.2 (32.5)	0.6 (0.1)	31.3	0.9 (0.2)	0.3 (0.2)	12.5	1.9 (1.0)	10.9 (3.4)
	long	7	100.0	162.3 (171.0)	0.6 (0.4)	85.7	39.1 (18.0)	5.4 (1.6)	71.4	6.7 (3.0)	123.9 (198.0)
West to east	short	3	100.0	6.0 (8.0)	28.3 (25.0)	66.7	0.0 (0.0)	2.3 (1.0)	0.0	0 (0)	0 (0)
	long	1	100.0	3 (3)	84 (84)	100.0	3 (3)	3 (3)	100.0	30 (30)	30 (30)

TABLE 3.—Abundance of zooplankton at the east and west ends of Naples Reef, southern California. For each collection, differences in abundance between ends of the reef were tested with a Mann-Whitney *U*-test.

Direction of current flow	Date 1977	Numbers Average no./m³ ± 95% CI				Biomass Average mg/m² ± 95% CI			
		No. samples	East	No. samples	West	No. samples	East	No. samples	West
East to west	19 Aug.	6	1,302.2 ± 101.3*	5	485.0 ± 260.7	6	34.8 ± 3.1*	5	14.0 ± 4.7
	29 Aug.	10	1,589.2 ± 265.3ns	10	1,467.5 ± 590.4	10	19.8 ± 2.3ns	10	19.7 ± 3.6
	15 Sept.	10	3,301.0 ± 375.9*	10	2,809.4 ± 214.7	10	48.1 ± 4.3**	10	37.2 ± 3.6
	21 Sept.	10	2,585.2 ± 423.9**	10	1,095.8 ± 278.5	10	32.0 ± 3.4**	10	19.8 ± 4.3
	29 Sept.	10	2,849.8 ± 407.2ns	7	2,272.2 ± 582.1	10	67.6 ± 7.7*	7	53.0 ± 6.6
	20 Oct.	10	3,277.5 ± 427.5**	10	1,573.5 ± 289.1	10	43.2 ± 4.8**	10	28.5 ± 2.9
West to east	7 Sept.	10	1,983.2 ± 323.2**	10	3,184.3 ± 253.8	10	41.7 ± 6.3**	10	54.7 ± 3.6
	11 Oct.	10	3,062.2 ± 737.0**	10	5,314.2 ± 539.9	10	44.3 ± 9.3*	10	57.9 ± 7.2

*$P \leq 0.05$; **$P \leq 0.01$; ns, not significant.

quickly migrated to the opposite end of the reef. I began the survey by counting fish at the west end. The current was flowing from the east and I did not count any adult blacksmith, although visibility averaged 12.2 m. I then started the survey at the east end and counted 81 adults, when the currents shifted and flowed from the west. While swimming the transects, I saw small schools of adults (5-15 individuals) moving toward the west (now incurrent) end. I returned to the boat and followed adults as they swam toward the west end, where I repeated the transects. Even though water visibility dropped to 5.0 m, I counted 43 adults over the area where, 2 h earlier, I had counted none.

The movements of halfgrown blacksmith were less clear. Counts were generally higher at the east end when the current came from the east (Table 2; Wilcoxon's signed-ranks test: short surveys, $P = 0.14$; long surveys, $P = 0.06$; short and long combined, $P = 0.05$). However, the pattern was inconsistent, and counts were actually greater at the west end in 3 of the 11 surveys in which halfgrown fish were sighted. The proportion of halfgrown fish at the east end averaged 0.90 (95% CI = 0.38-1.0). A similar inconsistency occurred when the current flowed from the west. All halfgrown fish counted were at the west end on the two short surveys in which they were seen, but the three individuals counted in the long survey were at the east end.

Juvenile blacksmith did not gather at the incurrent end. When the current flowed from the east, all juveniles were at the west end of the reef in the two short surveys in which they were seen and in the five long surveys (Table 2; Wilcoxon's signed-ranks test; long surveys, $P < 0.05$). The proportion of juveniles at the east end averaged only 0.03 (95% CI = 0-0.18). When the current flowed from the west, juveniles were not seen in the short surveys, and were equally abundant at both ends of the reef on the one long survey. However, these data do not accurately describe the response of juveniles to water currents. Observations along the bottom indicate that, regardless of the current direction, many juveniles occurred throughout the reef in stationary aggregations that form around shallow rocky prominences. The large number of juveniles counted at the west end reflected the location of the transects on the reef: almost 87% of the juveniles counted in the midwater surveys were seen in the two transects at the west end, which were the only transects over the shallowest part of the reef (Figure 1).

Zooplankton Densities

I took eight collections of zooplankton from mid-August to mid-October 1977 (Table 3). In six of the collections, the current flowed from the east; in the other two the current was reversed and flowed from the west.

Even though the counts of plankton were standardized to densities, I attempted to sample the same volume of water in each tow to make it equally likely that relatively rare items would be collected at both ends. In seven of eight collections, volumes of water sampled did not differ significantly between reef ends (t-tests, $P>0.10$); in the last collection a significantly greater volume of water was sampled at the west end of the reef ($P<0.01$). The average length of the tows was 57.1 m, which corresponds to a filtered volume of 11.2 m^3.

Small copepods (<4 mm carapace length) and cladocerans were the most abundant items in the samples, averaging 1,259/m^3 and 836/m^3. Small copepods dominated in 93 samples while cladocerans dominated in the remaining 55 samples. Most of the copepods were calanoids, although cyclopoids were also present. The majority of cladocerans appeared to be *Evadne* sp., but *Penilia* sp. occasionally dominated. Larvaceans ranked third in abundance, averaging 119.6/m^3.

Densities of zooplankton differed markedly between the incurrent and excurrent sample sites at Naples Reef. For each collection, mean number and dry weight of plankton pooled in excurrent samples were lower than those in incurrent samples, regardless of the current direction. Differences in counts were significant in six of the eight individual collections (Table 3), and for all eight collections tested together (Wilcoxon's signed-ranks test, $P<0.005$). Estimates of dry weights followed a similar pattern (Table 3).

The trend of a decreased abundance near the excurrent end was shared among many of the zooplankton groups (Table 4). Cladocerans, larvaceans, and bryozoan larvae were significantly less abundant at the excurrent end in seven of eight collections. Other groups were less abundant near the excurrent end in some collections but not in others. For example, densities of small copepods were significantly lower in excurrent samples in six collections, but were higher in another collection (Table 4). Overall, mean densities of 7 of the 15 plankton groups were significantly lower near the excurrent end. Cladocerans, small copepods, and larvaceans showed the greatest decrease near the excurrent end, while polychaetes and nauplii averaged slightly greater there.

Foraging Experiments

I attempted eight experiments between late July and mid-December 1977; three were deleted because several fish died in the cages. The following analysis is based on the 27 of 31 fish in the remaining five experiments that had food in their guts and showed no signs of injury. The first four experiments used larger individuals (117-214 mm SL); the last experiment used smaller fish (88-117 mm SL). For each experiment, there were only

TABLE 4.—Zooplankton densities near the incurrent and excurrent ends of Naples Reef, southern California. Densities are averaged among means of the eight collection days. Columns to the right indicate number of collections during which plankton densities at the incurrent end were greater, less than, or equal to those near the excurrent end (Mann-Whitney U-tests, two tailed; $P\leq0.05$). Symbols next to incurrent densities indicate P values from a one-tailed Wilcoxon's signed-ranks test for incurrent and excurrent differences in density among all collections combined. Plankton groups are listed in order of decreasing differences in densities between incurrent and excurrent ends of the reef.

Plankton group	Average number per m^3		Number of collections		
	Incurrent	Excurrent	Incurrent < excurrent	Incurrent > excurrent	Incurrent = excurrent
Cladocerans	1,097.2*	575.7	7	0	1
Small copepods	1,402.3ns	1,114.8	6	1	1
Larvaceans	178.7**	60.4	7	0	1
Echinoderm larvae	54.6ns	15.7	3	0	[1]2
Doliolids	41.8**	9.7	5	0	3
Chaetognaths	32.1*	16.9	6	0	2
Medusae	39.8**	25.0	5	0	3
Large copepods	22.8*	9.7	3	1	3
Bryozoan larvae	15.5**	4.3	7	0	[1]0
Fish larvae	3.4ns	1.3	2	1	5
Decapod larvae	3.3ns	2.0	1	0	[1]3
Zoea	5.0ns	4.4	0	0	[1]5
Ostracods	0.3—	0.2	0	0	[1]1
Nauplii	1.0ns	1.2	0	0	[1]2
Polychaetes	0.9ns	1.4	0	0	[1]3

*$P\leq0.05$; **$P\leq0.005$; ns, not significant; — insufficient data.
[1] Not present in all eight collections.

minor size differences between fish in incurrent and excurrent cages (Table 5). Also, when data were pooled among experiments to increase sample size, neither length, weight, nor volume of fish differed significantly between cages (t-tests, $P > 0.75$).

Gut fullness was greater for fish in the incurrent cage (Table 5). Average fullness for 13 incurrent

TABLE 5.—Diets of blacksmith in five cage experiments at the incurrent and near the excurrent ends of Naples Reef, southern California. Only individuals with food in their guts were included in the analyses. Fullness is defined in the text.

	Experiment dates, 1977									
	25 July-1 Aug.		3-12 Aug		15-22 Aug.		9-19 Sept.		11-18 Oct	
Item	Incurrent	Excurrent	Incurrent	Excurrent	Incurrent	Excurrent	Incurrent	Excurrent	Incurrent	Excurrent
No. fish: with food, empty	4,0	5,0	3,0	2,1	1,1	1,1	1,1	2,0	4,0	4,0
SL (mm): $\bar{x}$	157.8	165.0	182.7	188.5	175	150	123	121.7	100.5	95 8
Range	145-179	145-187	167-195	161-214				117-129	90-117	88-117
Fullness: $\bar{x}$	0.70	0.30	0.67	0.06	1.0	0.36	1.0	0.47	0.57	0.18
Range	0.37-0.90	0.12-0.54	0.35-1.00	0.04-0.09				0.12-0.82	0.29-1.00	0 05-0.32
Food items	Average number per fish									
Larvaceans	981.3	77.5	148.3		153		452	201.5	482.3	370.3
Large copepods			8.0		67		172	2.5	70.3	2.3
Small copepods	82.3	186.8	12.7		57	20	148	62.0	211.0	156.8
Cladocerans	26.0	20.4						1.0	17.8	29.0
Chaetognaths			6.7					0.5	2.3	0.8
Decapod larvae		0.5						1.0	10.3	0.5
Polychaetes			0.7		10		23	1.5	1.0	3.0
Fish larvae		0.5								
Obelia sp.		3.5		7.5		3				
Total items	1,089.6	289.2	176.4	7.5	287	23	795	270.0	795.0	562.7

TABLE 6.—Diets of free-living and caged blacksmith at the incurrent end of Naples Reef, southern California. Fullness is defined in the text.

	Collection date, 1977					
	29 Sept.		18 Oct.		6 Dec.	
Item	Caged	Free	Caged	Free	Caged	Free
No. fish: with food, empty	3,0	5,0	4,0	5,0	3,1	4,0
SL (mm): Mean	113.7	114.8	100.5	112.2	91.3	100.3
Range	110-118	100-121	90-117	94-127	86-98	91-107
Fullness: Mean	0.34	0.73	0.32	0.69	0.81	0.46
Range	0.30-0.39	0.48-1.00	0.14-0.58	0.41-1.00	0.78-1.00	0.32-0.59
Food items	Average number per fish					
Larvaceans	200.3	1,904.6	482.3	805.4	561.3	865.8
Large copepods	134.0	302.2	70.3	563.6	952.7	267.0
Small copepods	102.0	321.2	211.0	397.6	295.3	615.3
Cladocerans	1.3	150.4	17.8	26.0	14.3	28.8
Chaetognaths	1.3	34.8	2.3	24.6	4.3	13.0
Decapods	2.7	10.2	10.3	27.8	5.3	2.3
Polychaetes	1.7	20.0	1.0	5.8	1.0	2.0
Total items	444.3	2,743.4	795.0	1,850.8	1,834.2	1,794.2

TABLE 7.—Diets of free-living juvenile blacksmith collected near the incurrent and excurrent ends of Naples Reef, southern California. Fullness is defined in the text.

	Collection date, 1977					
	29 Sept.		18 Oct.		20 Mar.	
Item	Incurrent	Excurrent	Incurrent	Excurrent	Incurrent	Excurrent
No. fish: with food, empty	5,0	5,0	5,0	4,0	11,0	11,0
SL (mm): Mean	114.8	111.2	112.2	101.5	118.2	105.7
Range	100-121	85-117	94-127	85-116	101-122	98-114
Fullness: Mean	0.73	0 40	0.69	0.26	0.72	0.51
Range	0.48-1.00	0.04-0.61	0.41-1.00	0.02-0.83	0.62-0.93	0.02-0.81
Food items	Average number per fish					
Larvaceans	1,904.6	1,084.2	805.4	339.5	Not analyzed	
Large copepods	302.2	107.8	563.6	18.0		
Small copepods	321.2	292.8	397.6	313.3		
Cladocerans	150.4	207.2	26.0	34.5		
Chaetognaths	34.8	6.6	24.6	2.8		
Decapod larvae	10.2	4.6	27.8	8.0		
Polychaetes	20.0	8.6	5.8	1.3		
Total items	2,743.4	1,711.8	1,850.8	717.4		

fish, 0.70, was significantly greater than that for the 14 excurrent fish, 0.20 (Mann-Whitney U-test, $P < 0.001$).

Nine categories of food items were identified from gut contents of caged blacksmith (Table 5). Larvaceans and copepods predominated, while other groups were usually rare or absent. All items were typically planktonic except for the sessile stage of the hydrozoan, *Obelia* sp., which quickly colonized cages even though they were scrubbed before each experiment. *Obelia* sp. occurred in gut contents as small branches (< 5 mm long), and each was counted as one individual. Eliminating *Obelia* sp. would decrease gut fullness for excurrent fish even more (Table 5). Dietary variation between cages included differences in relative abundances of larvaceans and copepods, and additions of rare items in the excurrent cages. In the incurrent cage, larvaceans were the most abundant food items in all experiments, but in the excurrent cage, they were most abundant in only two experiments. When present, large copepods (>4 mm) were found mostly in incurrent-caged fish. Though relatively few in numbers, the size of these copepods (some nearly 10 mm long) probably made them nutritionally important. That excurrent fish ate *Obelia* sp. during three experiments is difficult to explain. Tufts of *Obelia* sp. may have been more abundant in the excurrent cages, because the excurrent cages appeared to foul at a faster rate. Sessile hydroids are not a normal food of blacksmith (Hobson and Chess 1976).

Caging altered the blacksmith diets, but the effects were variable. In two of three collections, free fish had generally consumed more food than caged fish (Table 6). Seven categories of food items were identified in the guts of caged and free fish. As before, larvaceans and copepods were by far the most abundant. Cladocerans were abundant in a few individuals, but chaetognaths, decapod larvae, and polychaetes were uncommon. Free fish ate mostly larvaceans in all of the collections, but caged fish were inconsistent. In one collection, caged fish ate mostly large copepods, but in the other two, they ate mostly larvaceans.

Free-living juveniles at the incurrent end ate more food than those at the excurrent end (Table 7). Pooled among collections, gut fullness differed significantly between reef ends (Mann-Whitney U-test, $P < 0.05$). Nonetheless, dietary composition of all free-living juveniles was similar. Larvaceans always made up the most abundant item, with copepods and cladocerans also common. Numbers of small copepods were slightly less in excurrent fish, but the difference was not nearly so great as for larvaceans or large copepods. Numbers of cladocerans were greater in excurrent fish.

DISCUSSION

Blacksmith Distribution Patterns

Adults

The midwater surveys indicate that large numbers of adult blacksmith (>150 mm TL) swim to the incurrent end of Naples Reef. Under the usual current pattern of flow from the east, almost all adults recorded were at the east end; when currents reversed, adults were far more abundant at the west end. During one survey, adults were actually seen migrating to the opposite end as currents reversed. The only times I saw large numbers of adults dispersed throughout the reef occurred when currents were negligible. On another occasion at Toyon Bay, Santa Catalina Island (190 km southwest of Naples Reef), I saw a similar response of blacksmith to a current reversal.

Observations at night indicate that large numbers of blacksmith of all sizes take shelter in holes at the west (usually the excurrent) end of Naples Reef. Indeed, the density of sheltering blacksmith at the west end may exceed that at the east because higher rocky relief and more complex substratum at the west end provide more refuges. An investigation of the sheltering behavior of tagged blacksmith indicated that many individuals tend to return to the same shelter at night (Bray in prep.). Yet when the current flowed from the east, extensive searches throughout the entire reef during the day failed to reveal substantial numbers of adults anywhere but at the east end. During the present midwater surveys, I saw one of these tagged fish in a feeding aggregation at the extreme eastern margin of the kelp, almost 300 m away from the hole where it was tagged. This, and my observation that blacksmith swam the length of the reef when currents reversed, indicates that some adults must swim a considerable distance each day to gather at the incurrent end.

Juveniles

In contrast, juvenile blacksmith (<125 mm TL)

apparently do not congregate at the incurrent end. Although midwater counts were highest at the excurrent end, bottom observations indicate that juveniles occur abundantly throughout the reef. Some form large stationary aggregations about reef prominences while others are more dispersed, hovering within a few meters of the rocky substratum. Halfgrown fish are most abundant along the reef edge, between aggregations of adults and juveniles. To simplify the transects, I tallied blacksmith as though they were comprised of two major size classes, juveniles and adults; halfgrown fish made up but a small group of intermediate-sized individuals that allowed clearer distinction between these two classes. Actually, fish sizes ranged almost continuously from small juveniles to large adults. The degree of fish movements vary accordingly, from very short forays of newly settled juveniles to extensive migrations of large adults.

Foraging at Incurrent End of the Reef

Adults

In synthesizing day and night observations of fish residing on temperate and tropical Pacific reefs, Hobson (1973) concluded that when fish are active their dominant behavior is feeding, and when they are inactive they seek security either by schooling or by sheltering. Hobson (1972) states, "A suitable feeding location for any given species may or may not be near areas that offer it suitable security during its inactive period. Consequently, the major actions of these fishes characteristic of twilight relate to moving between feeding locations and shelter locations."

The most suitable foraging site for adult blacksmith, in terms of food availability, is likely at the incurrent end of the reef. The paired caging experiments indicated that the amount of zooplankton consumed by adults at the incurrent end was greater than the amount eaten by those over the reef near the excurrent end. Although the caging procedure itself did influence blacksmith foraging, I assume the effect was similar in both cages, so the differences in gut fullness reflected the relative availability of food at the reef ends.

There are at least two possible reasons for the greater food abundance at the incurrent end. First, plankton is probably replenished there at a faster rate. Measurements of current velocities indicated that water crossing the reef is slowed and deflected by rocky prominences and columns of giant kelp. When feeding in a current, blacksmith often position themselves in areas of slack water behind kelp while currents deliver food (Hobson and Chess 1976). On the other hand, fish in relatively calm water at the excurrent end may have to swim about, possibly farther from kelp or other shelter, to encounter food at a comparable rate. Hobson and Chess (1976) observed that feeding rates of blacksmith were greater in a moderate than a slack current.

Second, the density of zooplankton is greater at the incurrent end. Under the normal pattern of current flow with water coming from the east, zooplankton densities were consistently greater at the east end of the reef. Even more convincing, however, was the effect of current reversal; on these two occasions, zooplankton densities were significantly greater at the west end, with most of the differences attributable to decreased densities of cladocerans, small copepods, and larvaceans. I feel that the plankton samples provided a good measure of the abundance of the blacksmith's potential prey because the most abundant items in the plankton samples (copepods, cladocerans, and larvaceans) were also the major items found in the blacksmith guts. Also, I sampled in areas where blacksmith normally gather in the appropriate current conditions, and I was invariably surrounded by foraging adults while I collected plankton at the incurrent end. Although several investigators have discussed decreased densities of plankton in kelp beds (Limbaugh 1955; Quast 1968b; Miller and Geibel 1973; Feder et al. 1974), to my knowledge, this is the first quantitative documentation.

Juveniles

The incurrent end of the reef would seem to be the most suitable foraging site for juveniles—at least those that forage here consume more prey, as determined by the caging experiments and examinations of free-living individuals. But the surveys showed that juveniles fail to concentrate here, which indicates that other factors override the advantages of incurrent foraging.

Optimization models may be used to interpret foraging movements of planktivorous fishes (Reese 1978). While the benefits of movements usually involve energy gains, costs may include a variety of factors, such as competition, expendi-

tures of time and energy, and the threat of increased predation (e.g., Pyke et al. 1977). The differences in foraging movements between juvenile and adult blacksmith may indicate that although juveniles apparently benefit from foraging at the incurrent end, the cost of migrating to and maintaining station at the incurrent end might outweigh the benefit of greater food intake there. Smaller fish have lower cruising speeds and expend relatively more energy in swimming a given distance (Bainbridge 1958, 1960), so juveniles sheltering at the excurrent end may find it too costly to swim across the reef. Juveniles already at the incurrent end may remain near the bottom, because they find it too costly to maintain station in strong midwater currents. Hobson and Chess (1976) observed that in strong currents, blacksmith abandon open places for the lee of kelp plants. Similarly, when currents are strong over tropical reefs, diurnal planktivores approach the bottom (Hobson and Chess 1978).

Predation pressures may limit the movements of juveniles, which are vulnerable to many more predators than are the adults. Covich (1976:242) presented a simple graphic model that showed how predation can influence distances traveled by foragers if the threat of predation increased farther away from shelter; he stated, "Often the risk of predation to the forager and the distribution of resources are the major interacting variables that regulate consumer movement." In the tropics, juvenile fishes remain closer to reefs than adults, and at dusk when predation is most intense, smaller individuals seek shelter first (Hobson 1972, 1979). Many coral reef fish seek nearby shelter when predators approach (e.g., Hartline et al. 1972), and relocation experiments indicate that damselfishes released away from shelter are quickly eaten (Mariscal 1970; Nolan 1975). Similarly, the threat of predation might discourage juvenile blacksmith from aggregating in midwater at the incurrent end of Naples Reef. *Paralabrax clathratus* ranked second in abundance in my midwater surveys (Table 1), with larger individuals tending toward the incurrent end. Although these predators may exceed 700 mm TL (Miller and Lea 1972), they probably would have difficulty consuming large blacksmith. However, I have observed kelp bass >400 mm TL attacking juveniles, and gut analyses indicate they feed on a variety of small fishes, including juvenile blacksmith (Quast 1968d; Love and Ebeling 1978). Additional predators include other residential as well as open-water fishes, and marine birds and mammals.

Zooplankton Distribution Patterns

Residents Versus Nonresidents

Comparing differences in plankton densities across a reef has often been used to estimate the importance of plankton to the energetics of reef communities (e.g., Johannes and Gerber 1974). However, others have shown that inshore reefs also contain resident zooplankters with different habitat preferences. Many of these "demersal plankters" form a nocturnal component that either hides in the reef during the day and emerges at night (e.g., Alldredge and King 1977) or resides in deeper water during the day and moves into shallow areas at night (Hobson and Chess 1978, 1979). Thus, as several authors have pointed out (e.g., Alldredge and King 1977), differences in plankton densities across a reef might reflect the habitat preferences or patchiness of resident zooplankton, rather than the consumption of extrinsic zooplankton by fish or other reef residents.

It is doubtful that the incurrent-excurrent differences in plankton densities at Naples Reef resulted from sampling resident, demersal zooplankton. All samples were taken around midday in the water column away from reef or kelp substrata. At this time, most demersal forms hide in or near shelter or in deeper water (Alldredge and King 1977; Hobson and Chess 1976, 1978, 1979). Furthermore, typical reef residents—mysids, cumaceans, polychaetes, and decapods—were insignificant components in the plankton collections, while the groups that were consistently less abundant at the excurrent end—cladocerans and larvaceans—have not been reported as residential forms. However, it would be risky to conclude that the observed decline in zooplankton density across Naples Reef was entirely a consequence of predation by fishes and invertebrates of the kelp-bed community. I did not follow a specific parcel of water as it drifted across the reef; in fact, I sampled the excurrent end of the reef first in five of eight collections. Thus, at least some of the differences in plankton densities between the two ends may have been due to my sampling different patches of plankton. This would explain, e.g., the greater numbers of small copepods at the excurrent end in one collection (Table 4).

Impact of Blacksmith Foraging

Most of the food consumed by blacksmith comes from outside the reef community. Blacksmith diets, of course, depend on the composition of the plankton, but consist largely of larvaceans, cladocerans, and copepods. The same items dominate the diet of blacksmith off Santa Catalina Island (Hobson and Chess 1976). Some copepods may be members of the reef community (as discussed above), but the small calanoids in the blacksmith's diet are more likely a part of the drift plankton; residential forms probably would not occur during the day in the exposed, current-swept midwater areas of the incurrent end of the reef.

Too little is known about the total population and daily food consumption of blacksmith, and about the amount of plankton that passes over the reef, to accurately assess the effect of blacksmith foraging on incoming zooplankton. However, several lines of evidence indicate that blacksmith are major predators. The dominant items in their diets are those that showed the greatest decrease in abundance. Also, individual blacksmith consume a large amount of food each day. The guts of blacksmith are empty at dawn (Hobson and Chess 1976; Bray unpubl. data), so guts of individuals collected at dusk contain food that was consumed that day. The number of plankters in the stomach of 14 blacksmith (124-178 mm SL) that were speared as they sheltered at dusk averaged 1,455 items, 95% of which were larvaceans and small copepods. And these data underestimate the total number consumed. They exclude intestinal items, even though these largely unidentifiable remains weighed an average of 2.2 times the contents of the stomach, and they ignore items evacuated before dusk. Thus, considering that blacksmith composed over 42% of the 7,800 fish tallied, I conclude along with Limbaugh (1955) that they materially affect the plankton that is swept across southern California kelp beds.

ACKNOWLEDGMENTS

I thank Alfred Ebeling for his guidance and support throughout this project. Many people generously assisted me in the field, but I especially appreciate the help of Jeff Bovee and Philippe Vigneaud. Discussions with Tom Bailey and Ralph Larson provided many ideas. Norm Lammer and Jack Kisch kept the boats running. Larry Leamy helped with the statistics, and Laurie Farmer, Esther Escandón, and Michelle Smith assisted in gut analyses and preparation of the final manuscript. Alice Alldredge, Joseph Connell, and Michael Neushul offered excellent suggestions during the project and, along with Edmund Hobson and an anonymous referee, critically reviewed earlier drafts. Finally, I thank my wife, Cindy, for her help, encouragement, and tolerance. Financial support was provided by NOAA, Office of Sea Grant, Department of Commerce, under grants 2-35208-6 and 04-3-158-22 (Project R-FA-14), by NSF grants GA 38588 and OCE 76-23301, and Sea Grants GH 43 and GH 95, all to Alfred Ebeling. Additional funding at the University of California, Santa Barbara, was provided by Henry Offen, Director of the Marine Science Institute.

LITERATURE CITED

ALLDREDGE, A. L., AND J. M. KING.
1977. Distribution, abundance, and substrate preferences of demersal reef zooplankton at Lizard Island Lagoon, Great Barrier Reef. Mar. Biol. (Berl.) 41:317-333.

BAINBRIDGE, R.
1958. The speed of swimming of fish as related to size and to the frequency and amplitude of the tail beat. J. Exp. Biol. 35:109-133.
1960. Speed and stamina in three fish. J. Exp. Biol. 37:129-153.

COLLETTE, B. B., AND F. H. TALBOT.
1972. Activity patterns of coral reef fishes with emphasis on nocturnal-diurnal changeover. *In* B. B. Collette and S. A. Earle (editors), Results of the Tektite program: ecology of coral reef fishes, p. 98-124. Nat. Hist. Mus. Los Ang. Cty., Sci. Bull. 14.

COVICH, A. P.
1976. Analyzing shapes of foraging areas: some ecological and economic theories. Annu. Rev. Ecol. Syst. 7:235-257.

DE BOER, B. A.
1978. Factors influencing the distribution of the damselfish *Chromis cyanea* (Poey), Pomacentridae, on a reef at Curacao, Netherlands Antilles. Bull. Mar. Sci. 28: 550-565.

EBELING, A. W., AND R. N. BRAY.
1976. Day versus night activity of reef fishes in a kelp forest off Santa Barbara, California. Fish. Bull., U.S. 74:703-717.

EBELING, A. W., R. J. LARSON, W. S. ALEVIZON, AND R. N. BRAY.
1980. Annual variability of reef-fish assemblages in kelp forests off Santa Barbara, California. Fish. Bull., U.S. 78:361-377.

EMERY, A. R.
1973. Comparative ecology and functional osteology of fourteen species of damselfish (Pisces: Pomacentridae) at Alligator Reef, Florida Keys. Bull. Mar. Sci. 23:649-770.

FEDER, H. M., C. H. TURNER, AND C. LIMBAUGH.
1974. Observations on fishes associated with kelp beds in southern California. Calif. Dep. Fish Game, Fish Bull. 160, 144 p.

HARTLINE, A. C., P. H. HARTLINE, A. M. SZMANT, AND A. O. FLECHSIG.
1972. Escape response in a pomacentrid reef fish, *Chromis cyaneus*. *In* B. B. Collette and S. A. Earle (editors), Results of the Tektite program: ecology of coral reef fishes, p. 93-97. Nat. Hist. Mus. Los Ang. Cty., Sci. Bull. 14.

HOBSON, E. S.
1965. Diurnal–nocturnal activity of some inshore fishes in the Gulf of California. Copeia 1965:291-302.
1972. Activity of Hawaiian reef fishes during the evening and morning transitions between daylight and darkness. Fish. Bull., U.S. 70:715-740.
1973. Diel feeding migrations in tropical reef fishes. Helgol. wiss. Meeresunters. 24:361-370.
1974. Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. Fish. Bull., U.S. 72:915-1031.
1979. Interactions between piscivorous fishes and their prey. *In* H. E. Clepper (editor), Predator-prey systems in fisheries management, p. 231-242. Sport Fishing Inst., Wash., D.C.

HOBSON, E. S., AND J. R. CHESS.
1976. Tropic interactions among fishes and zooplankters near shore at Santa Catalina Island, California. Fish. Bull., U.S. 74:567-598.
1978. Trophic relationships among fishes and plankton in the lagoon at Enewetak Atoll, Marshall Islands. Fish. Bull., U.S. 76:133-153.
1979. Zooplankters that emerge from the lagoon floor at night at Kure and Midway Atolls, Hawaii. Fish. Bull., U.S. 77:275-280.

JOHANNES, R. E., AND R. GERBER.
1974. Import and export of net plankton by an Eniwetok coral reef community. Proc. 2d Int. Symp. Coral Reefs 1:97-104.

LIMBAUGH, C.
1955. Fish life in the kelp beds and the effects of kelp harvesting. Univ. Calif., Inst. Mar. Res., IMR Ref. 55-9, 158 p.

LOVE, M. S., AND A. W. EBELING.
1978. Food and habitat of three switch-feeding fishes in the kelp forests off Santa Barbara, California. Fish. Bull., U.S. 76:257-271.

MARISCAL, R. N.
1970. The nature of the symbiosis between Indo-Pacific anemone fishes and sea anemones. Mar. Biol. (Berl.) 6:58-65.

MILLER, D. J., AND J. J. GEIBEL.
1973. Summary of blue rockfish and lingcod life histories; a reef ecology study; and giant kelp, *Macrocystis pyrifera*, experiments in Monterey Bay, California. Calif. Dep. Fish Game, Fish Bull. 158, 137 p.

MILLER, D. J., AND R. N. LEA.
1972. Guide to the coastal marine fishes of California. Calif. Dep. Fish Game, Fish Bull. 157, 235 p.

NOLAN, R. S.
1975. The ecology of patch reef fishes. Ph.D. Thesis, Univ. California, San Diego, 246 p.

PYKE, G. H., H. R. PULLIAM, AND E. L. CHARNOV.
1977. Optimal foraging: a selective review of theory and tests. Q. Rev. Biol. 52:137-154.

QUAST, J. C.
1968a. Some physical aspects of the inshore environment, particularly as it affects kelp-bed fishes. *In* W. J. North and C. L. Hubbs (compilers and editors), Utilization of kelp-bed resources in southern California, p. 25-34. Calif. Dep. Fish Game, Fish Bull. 139.
1968b. Fish fauna of the rocky inshore zone. *In* W. J. North and C. L. Hubbs (compilers and editors), Utilization of kelp-bed resources in southern California, p. 35-55. Calif. Dep. Fish Game, Fish Bull. 139.
1968c. Observations on the food and biology of the kelp bass, *Paralabrax clathratus*, with notes on its sport-fishery at San Diego, California. *In* W. J. North and C. L. Hubbs (compilers and editors), Utilization of kelp-bed resources in southern California, p. 81-108. Calif. Dep. Fish Game, Fish Bull. 139.
1968d. Effects of kelp harvesting on the fishes of the kelp beds. *In* W. J. North and C. L. Hubbs (compilers and editors), Utilization of kelp-bed resources in southern California, p. 143-149. Calif. Dep. Fish Game, Fish Bull. 139.

REESE, E. S.
1978. The study of space-related behavior in aquatic animals: special problems and selected examples. *In* E. S. Reese and F. J. Lighter (editors), Contrasts in behavior. Adaptations in the aquatic and terrestrial environments, p. 347-374. Wiley, N.Y.

SALE, P. F.
1971. Extremely limited home range in a coral reef fish, *Dascyllus aruanus* (Pisces: Pomacentridae). Copeia 1971:324-327.

STEVENSON, R. A., JR.
1972. Regulation of feeding behavior of the bicolor damselfish (*Eupomacentrus partitus* Poey) by environmental factors. *In* H. E. Winn and B. L. Olla (editors), Behavior of marine animals. Vol 2: Vertebrates, p. 278-302. Plenum Press, N.Y.

ESTIMATED INITIAL POPULATION SIZE OF THE BERING SEA STOCK OF BOWHEAD WHALE, *BALAENA MYSTICETUS*: AN ITERATIVE METHOD

JEFFREY M. BREIWICK,[1] EDWARD D. MITCHELL,[2] AND DOUGLAS G. CHAPMAN[3]

ABSTRACT

Initial stock sizes of bowhead whales were calculated iteratively, using an estimate of removals from the Bering Sea stock of bowheads, a range of assumed values for size of current stock, and assumed mortality and recruitment rates of $M = 0.04-0.08$ and $(r-M)_{max} = 0.01-0.05$. Estimates of initial stock size range between 14,000 and 26,000. At a kill level of 25 per annum, time to recover to 9,000 (50% of 18,000) is a minimum of 40 years if the present stock is approximately 2,700 bowheads. A theoretical model giving the risk of extinction is also discussed.

The International Whaling Commission has recently established quotas on the aboriginal take of the bowhead whale, *Balaena mysticetus*, in the Bering, Chukchi, and Beaufort Seas. This has led to much discussion of the status of the stock both now and in relation to its original size.

Bowhead whales are distributed throughout the Arctic in several presumably discrete stock units. Tomilin (1957) recognized four circumpolar stock units and Mitchell[4] identified five. Regardless of various interpretations, the Bering-Chukchi-Beaufort Sea stock has been regarded by all authors for many years as a discrete stock (Figure 1).

This stock winters in the Bering Sea, but during the spring it moves through the Bering Strait along the northwestern and northern coasts of Alaska at least as far as the Beaufort Sea. The Beaufort and Chukchi Seas are the main feeding areas. For convenience we will refer to this stock hereafter as the Bering Sea stock. This paper concentrates solely on this stock, for which commercial exploitation began in 1848, the date to which "initial" but not "unexploited" stock refers. Eskimo utilization of bowhead whales dates back many centuries, hence the Bering Sea stock was subject to human influence prior to 1848.

After 1848 the Bering Sea stock was rapidly depleted by heavy commercial exploitation—thus following a pattern that had been established earlier with respect to the Spitzbergen, Davis Strait, and Hudson Bay stocks and which also was to occur with the putative Okhotsk Sea stock (Mitchell footnote 4). Of all these depleted stocks, that of the Bering Sea is now the most abundant, and the only one from which removals of any consequence are occurring.

There are few satisfactory estimates of current population size for other bowhead whale stocks; estimates of the population sizes of all stocks at the onset of heavy commercial exploitation are even less reliable. Accordingly, we here present one approach to verify the order of magnitude of the early Bering Sea stock. We have also used some assumed estimates of the vital parameters in a simulation study of the expected time of recovery of this stock with catches at the present level.

The basis of the method is to start with an assumed current stock size and a recruitment rate, which is a function of stock size. The same form for the recruitment function is used throughout—a linear function decreasing from its maximum value at zero stock level to the natural mortality rate, M, at the initial stock level. Given current stock size, maximum net recruitment rate, mortality rate, and lag time between birth and age at recruitment into the fishery, the program starts with an estimated initial (1848) level. The pro-

[1]College of Fisheries, University of Washington, Seattle, Wash.; present address: Northwest and Alaska Fisheries Center National Marine Mammal Laboratory, National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE., Seattle, WA 98115.

[2]Arctic Biological Station, 555 St.-Pierre Blvd., Ste. Anne de Bellevue, Quebec, Canada H9X 3R4.

[3]College of Fisheries, University of Washington, Seattle, WA 98195.

[4]Mitchell, E. D. 1977. Initial population size of bowhead whale (*Balaena mysticetus*) stocks: cumulative catch estimates. Int. Whal. Comm. Doc. SC/29/33, 112 p. The Red House, Station Road, Histon, Cambridge CB4 4NP, Engl.

Manuscript accepted March 1980.
FISHERY BULLETIN: VOL. 78, No. 4, 1981.

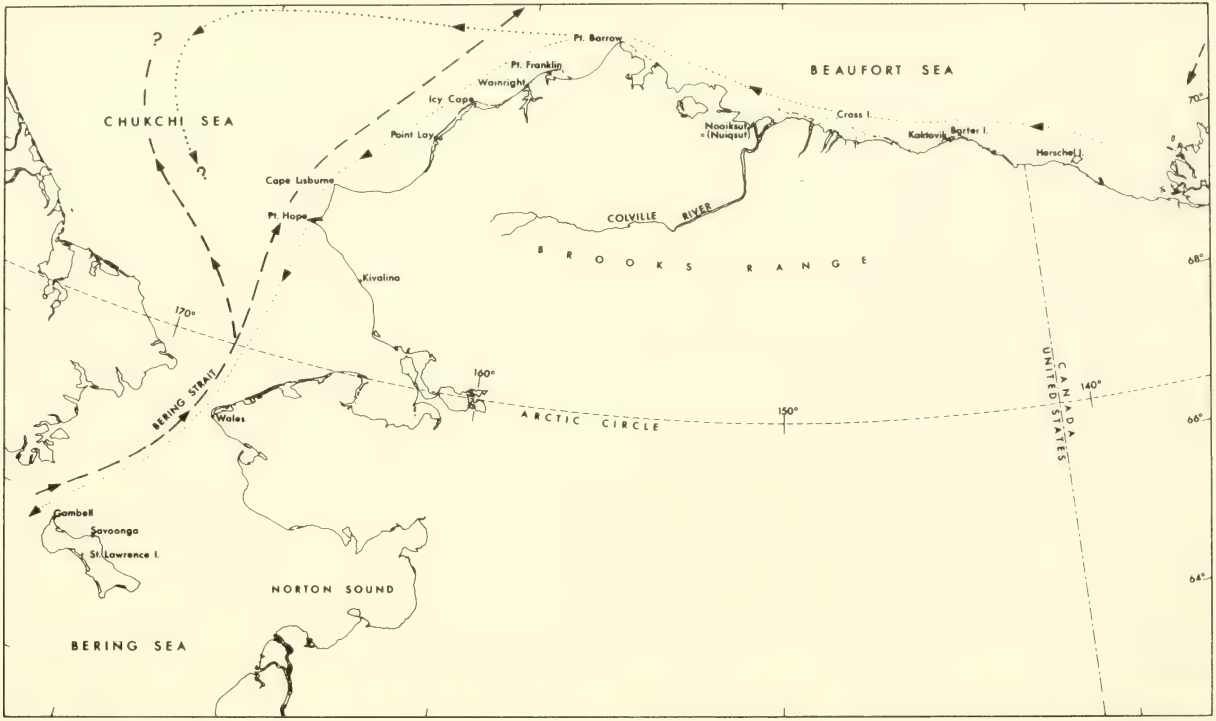


FIGURE 1.—Northern Alaska and adjacent waters, showing villages where recent whaling activities occur, and general migration trend of the bowhead whale. Dashed line, spring migration into Chukchi Sea, to summering grounds of Beaufort Sea and Amundsen Gulf; dotted line, fall migration to Chukchi Sea, and southward to Bering Sea. Bowhead migration routes based on Townsend (1935, chart D) and data of Cook (1926) as plotted in Sergeant and Hoek (1974, fig. 1).

gram then calculates forward and adjusts the initial level until it yields the correct (i.e., assumed) current stock size. Current population estimates are based on sightings and therefore are presumably for the total population.

In order to reconstruct the 1848 level, it is necessary to have a record of the catch history since that time, together with a reasonable range of estimates of the other parameters noted, i.e., mortality rate, maximum net recruitment rate, and current population size. Estimated catches and other assumed parameter values are discussed below.

METHODS

Stock Size Analysis

Estimates of Initial Stock Size

Rice (1974), using data of Clark (1887), estimated a Bering Sea stock size of 4,000-5,000 animals during a peak harvest from 1868 to 1884. Mitchell (footnote 4) concluded that the period of peak catch was earlier and, after examining methods of extrapolating catch from production statistics (oil and baleen yield) and catch per vessel, constructed a catch history (1849-1976) based on these estimates or on known catch. Mitchell summed the cumulative catch for the peak decade (1851-60), applied a loss rate of 24%, and concluded that a minimum population of 11,647 bowheads existed in 1850. He then performed the same cumulative catch summation on what he termed the "residual stock," which had survived, and exploitation of which had resulted in another peak catch period in the 1880's-1890's.

In summing the two cumulative catch estimates of population size, Mitchell corrected the latter by subtracting from it an assumed net recruitment of 5% per year over the period between the peaks. He concluded that the initial stock must have comprised approximately 18,000 bowhead whales. The calculations discussed below are a refinement of this rough procedure and show that this estimate is not unreasonable.

Catch History

We have taken the best estimate of commercial catch for each year or the known catch when available, and applied the struck but lost (and assumed moribund) rates estimated by Mitchell (footnote 4). We have added to these commercial removals the known aboriginal catch (Maher and Wilimovsky 1963; Durham 1979) with some additions (Marquette 1976, see footnotes 5 and 6; Mitchell footnote 4) and adjusted by the struck but lost (and assumed moribund) rates estimated by Mitchell (footnote 4). These are summarized in Table 1 (cf. Mitchell's table 9) for the entire period 1848-1977 (see footnotes under Mitchell's table for discussion of extrapolations and modifications to these data).

Estimates of Current Stock Size

There have been few recent surveys or counts which give quantitative estimates of total population abundance. Counts, e.g., from ice edge sightings through the season, were made by Braham and Krogman,[7] who estimated the 1976 inshore migration from 25 April to 2 June to include 796 animals. Breiwick and Chapman[8] extrapolated these data to account for animals that migrated earlier than 25 April or later than 2 June and arrived at a total population of 1,227. However, a more complete and careful census was carried out in 1978, in which whales were counted in the nearshore lead as they passed Barrow, Alaska, between 15 April and 30 May. The estimate for this component of the population was 2,264 (Braham et al. 1979). Aerial surveys were conducted in offshore leads and no whales were observed. In the model below we assumed 1978 stock levels of 900, 1,500, 2,100, and 2,700 animals.

Vital Parameters

As stated above, we assume a recruitment model with appropriate parameter values. If natural mortality is assumed to be fixed and the net recruitment rate is a linear function of stock size, the

[5]Marquette, W. M. 1976. National Marine Fisheries Service field studies relating to the bowhead whale harvest in Alaska, 1975. Processed Rep., 31 p. Natl. Mar. Mammal Lab., Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE., Seattle, WA 98115.

[6]Marquette, W. M. 1978. The 1976 catch of bowhead whales (*Balaena mysticetus*) by Alaskan Eskimos, with a review of the fishery 1973-1976, and a biological summary of the species. Processed Rep., 80 p. Natl. Mar. Mammal Lab., Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE., Seattle, WA 98115.

[7]Braham, H. W., and B. D. Krogman. 1977. Population biology of the bowhead (*Balaena mysticetus*) and beluga (*Delphinapterus leucas*) whales in the Bering, Chukchi and Beaufort Seas. Processed Rep., 29 p. Natl. Mar. Mammal Lab., Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE., Seattle, WA 98115.

[8]Breiwick, J. M., and D. G. Chapman. 1977. Population analysis of the Alaska bowhead whale stock. Int. Whal. Comm. Doc. SC/SPC/13, 5 p. The Red House, Station Road, Histon, Cambridge CB4 4NP, Engl.

TABLE 1.—Estimated pelagic and Eskimo kill of bowhead whales from the Bering Sea stock.

	American pelagic fishery			Eskimo fishery					American pelagic fishery			Eskimo fishery			
Year	Catch	Loss rate[1]	Kill subtotal	Known kill[2]	Loss rate	Kill subtotal	Kill total	Year	Catch	Loss rate[1]	Kill subtotal	Known kill[2]	Loss rate	Kill subtotal	Kill total
1848	25	0.24	31	—	0.24	0	31	1913	15	0.24	19	5	0.56	8	27
1849	1,061	0.24	1,316	—	0.24	0	1,316	1914	—	—	—	4	0.56	6	6
1850	1,061	0.24	1,440	—	0.24	0	1,440	1915	—	—	—	3	0.56	5	5
1851	597	0.24	740	—	0.24	0	740	1916	—	—	—	14	0.56	22	22
1852	1,912	0.24	2,371	17	0.24	21	2,392	1917	—	—	—	15	0.56	23	23
1853	1,482	0.24	1,838	7	0.24	9	1,847	1918	—	—	—	9	0.56	14	14
1854	1,326	0.24	1,644	—	0.24	0	1,644	1919	—	—	—	4	0.56	6	6
1855	1,315	0.24	1,631	—	0.24	0	1,631	1920	—	—	—	14	0.56	22	22
1856	1,040	0.24	1,290	—	0.24	0	1,290	1921	—	—	—	2	0.56	3	3
1857	819	0.24	1,016	—	0.24	0	1,016	1922	—	—	—	17	0.56	27	27
1858	975	0.24	1,209	—	0.24	0	1,209	1923	—	—	—	3	0.56	5	5
1859	811	0.24	1,006	—	0.24	0	1,006	1924	—	—	—	29	0.56	45	45
1860	549	0.24	681	—	0.24	0	681	1925	—	—	—	32	0.56	50	50
1861	412	0.24	511	—	0.24	0	511	1926	—	—	—	18	0.56	28	28
1862	158	0.24	196	—	0.24	0	196	1927	—	—	—	7	0.56	11	11
1863	307	0.24	381	—	0.24	0	381	1928	—	—	—	11	0.56	17	17
1864	364	0.24	451	—	0.24	0	451	1929	—	—	—	16	0.56	25	25
1865	348	0.24	432	—	0.24	0	432	1930	—	—	—	7	0.56	11	11
1866	551	0.24	683	—	0.24	0	683	1931	—	—	—	18	0.56	28	28
1867	569	0.24	706	—	0.24	0	706	1932	—	—	—	7	0.56	11	11
1868	450	0.24	558	—	0.24	0	558	1933	—	—	—	5	0.56	8	8
1869	395	0.24	490	—	0.24	0	490	1934	—	—	—	4	0.56	6	6
1870	490	0.24	608	—	0.24	0	608	1935	—	—	—	6	0.56	9	9
1871	75	0.24	93	—	0.24	0	93	1936	—	—	—	10	0.56	16	16
1872	186	0.24	231	—	0.24	0	231	1937	—	—	—	15	0.56	23	23
1873	162	0.24	201	—	0.24	0	201	1938	—	—	—	11	0.56	17	17
1874	160	0.24	198	—	0.24	0	198	1939	—	—	—	8	0.56	12	12
1875	173	0.24	215	—	0.24	0	215	1940	—	—	—	12	0.56	19	19
1876	57	0.24	71	—	0.24	0	71	1941	—	—	—	23	0.56	36	36
1877	102	0.24	126	—	0.24	0	126	1942	—	—	—	11	0.56	17	17
1878	74	0.24	92	—	0.24	0	92	1943	—	—	—	7	0.56	11	11
1879	130	0.24	161	5	0.24	6	167	1944	—	—	—	2	0.56	3	3
1880	265	0.24	329	7	0.56	11	340	1945	—	—	—	12	0.56	19	19
1881	170	0.24	211	18	0.56	28	239	1946	—	—	—	12	0.56	19	19
1882	170	0.24	211	1	0.56	2	213	1947	—	—	—	11	0.56	17	17
1883	170	0.24	211	2	0.56	3	214	1948	—	—	—	5	0.56	8	8
1884	170	0.24	211	10	0.56	16	227	1949	—	—	—	6	0.56	9	9
1885	170	0.24	211	40	0.56	62	273	1950	—	—	—	9	0.56	14	14
1886	170	0.24	211	—	0.56	0	211	1951	—	—	—	14	0.56	22	22
1887	170	0.24	211	11	0.56	17	228	1952	—	—	—	4	0.56	6	6
1888	170	0.24	211	3	0.56	5	216	1953	—	—	—	23	0.56	36	36
1889	170	0.24	211	7	0.56	11	222	1954	—	—	—	4	0.56	6	6
1890	170	0.24	211	2	1.00	4	215	1955	—	—	—	23	0.56	36	36
1891	184	0.24	228	19	1.00	38	266	1956	—	—	—	7	0.56	11	11
1892	201	0.24	249	8	1.00	16	265	1957	—	—	—	3	0.56	5	5
1893	193	0.24	239		1.00	0	239	1958	—	—	—	2	0.56	3	3
1894	118	0.24	146	13	1.00	26	172	1959	—	—	—	1	0.56	2	2
1895	70	0.24	87	4	1.00	8	95	1960	—	—	—	19	0.56	30	30
1896	25	0.24	31	39	1.00	78	109	1961	—	—	—	10	0.56	16	16
1897	173	0.24	215	5	1.00	10	225	1962	—	—	—	12	0.56	19	19
1898	21	0.24	26	27	1.00	54	80	1963	—	—	—	10	0.56	16	16
1899	154	0.24	191		1.00	0	191	1964	—	—	—	16	0.56	25	25
1900	62	0.24	77	19	1.00	38	115	1965	—	—	—	7	0.56	11	11
1901	11	0.24	14	1	0.56	2	16	1966	—	—	—	15	0.56	23	23
1902	63	0.24	78	2	0.56	3	81	1967	—	—	—	4	0.56	6	6
1903	58	0.24	72	8	0.56	12	84	1968	—	—	—	17	0.56	27	27
1904	44	0.24	55	3	0.56	5	60	1969	—	—	—	19	0.56	30	30
1905	41	0.24	51	7	0.56	11	62	1970	—	—	—	25	0.56	39	39
1906	5	0.24	6	6	0.56	9	15	1971	—	—	—	24	0.48	36	36
1907	58	0.24	72	9	0.56	14	86	1972	—	—	—	38	0.48	56	56
1908	20	0.24	25	47	0.56	73	98	1973	—	—	—	37	0.48	55	55
1909	28	0.24	35	25	0.56	39	74	1974	—	—	—	20	0.48	30	30
1910	6	0.24	7	2	0.56	3	10	1975	—	—	—	15	0.48	22	22
1911	72	0.24	89	4	0.56	6	95	1976	—	—	—	48	0.48	71	71
1912	0	0.24	0	3	0.56	5	5	1977	—	—	—	32	—	111	[3]111
								Total	21,823		27,068	1,234		2,025	29,093

[1]100% moribund in those lost.
[2]Includes "commercial" shore-based landings in later years.
[3]29 killed + recovered; 3 killed + lost; 79 struck + lost.

resulting recruitment in numbers generates a logistic relationship. At initial stock levels the recruitment rate is assumed to be equal to the natural mortality rate (which includes a small amount of exploitation mortality at the pre-1848 level). As the stock is reduced, recruitment rate

increases proportionally, attaining its maximum level when the stock is near zero. However, it is also recognized that response in rate may occur with some lag and thus various lag periods are assumed.

In order to construct the model, various parameter estimates are needed. These are discussed below.

Net Recruitment Rate

Since information on the maximum net recruitment rate is lacking, a range of values (0.01-0.05) was used, based on analogy with other baleen whale stocks for which such data are available. For example, Allen (1972) showed calculated rates for the fin whale, *Balaenoptera physalus*, (as a proportion of exploited stock) to be mostly in the range 0.021-0.036. The Scientific Committee of the International Whaling Commission (International Whaling Commission 1978) calculated maximum gross recruitment rates for the sei whale, *B. borealis*, (as a proportion of exploited female stock) as 0.26 which implies a net recruitment rate of the exploited stock to be 0.06. If we express these rates as a proportion of the total stock, they are in the range of 0.01-0.05. (Furthermore, estimates of the 1848 stock level became unstable and did not converge if maximum net recruitment rates >0.05 were used in our iteration.)

Natural Mortality

Similarly, there is no information available on natural mortality in bowheads, and a range of values of 0.04-0.08 was used. These correspond to mortality estimates for other baleen species (Doi et al. 1967; International Whaling Commission 1971).

Lag Time

We have no data on the growth and age of this species, and there were no regulations in the fishery. Nor do we have any information on the lag that may occur between the reduction of stock density and response of the population through its presumed increase in recruitment. In a similar study carried out for porpoise stocks involved in the yellowfin tuna purse seine fishery (National Marine Fisheries Service[9]), lag periods of 1, 3, and 5 yr were used. Because the population response in larger animals might be delayed, we have arbitrarily tried four lag periods: 1, 3, 5, and 7 yr. As will be shown, this parameter has minor effect.

Model Development

The assumptions outlined above can be formulated in mathematical terms as follows. The recruitment model is

$$r_t = M + (1 - P_{t-\tau}/P_0)(r - M)_{\max}, \quad (1)$$

where r_t = recruitment rate in season t
$P_{t-\tau}$ = population size at the beginning of season $t - \tau$ (τ = lag time assumed for population response)
P_0 = initial population size (start of 1848 season)
M = natural mortality rate
$(r - M)_{\max}$ = maximum net recruitment rate.

The extrapolation model also uses the (approximate) recursion formula (Allen 1966):

$$P_{t+1} = (P_t - C_t)e^{-M} + R_t \quad (2)$$

where $R_t = r_t P_{t-\tau}$ is the gross recruitment between the beginning of season t and season $t + 1$, and C_t, P_t are catch in season t and population size at the beginning of season t. A further approximation made is that $e^{-M} = 1 - M$. Equation (2) provides a good approximation if the catching season is relatively short and natural mortality is low.

The iterative procedure consists of specifying a current stock level, natural mortality rate, maximum net recruitment rate, and iterating on P_0 in Equation (2). Thus

$$P_n = g(P_0, P_1, \ldots, P_{n-1}) \quad (3)$$

where P_n is some current stock level. Due to the lag time involved in Equation (2), it is not practical to invert Equation (3) and solve for P_0 explicitly; hence the iterative solution of Equation (3) is obtained.

[9]National Marine Fisheries Service. 1976. Report of the workshop on stock assessment of porpoises involved in the eastern Pacific yellowfin tuna fishery. Adm. Rep. LJ-76-29, 54 p. Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, PO. Box 271, La Jolla, CA 92038.

Risk Analysis

For any population there is a positive probability of its extinction, though for most populations this is negligibly small. However, the probability will increase as the population size is reduced, e.g., by direct or indirect action of man. Such direct action may be a harvest which is uncontrolled or one which is controlled by fixed rules that do not consider stochastic fluctuations in the environment.

Random fluctuations in the environment or population which cause increased mortality or reduced births can lead to extinction, particularly if the population is at a very low level. Moreover, the longer the population is maintained there, the greater the probability of extinction. Such risks of extinction have for a long time been the subject of study in population theory, but most such models are rather simple and include only statistical variation within the population but not externally imposed stresses. We now develop a model that expresses probabilities of extinction as a function of average population growth and variability of environmental stresses. In this model we assume that there is an average increment for each year but, superimposed on this, a variability of the environment which may result in the actual change being positive or negative. We define a stochastic process which is the sum of annual increments which are normally distributed with mean μ and variance σ^2, and with successive increments independent. It is known from the theory of stochastic processes (c.f., Cox and Miller 1965:58) that the probability of the process being absorbed by barriers at levels "a" above the initial value or "b" below the initial value are equal to

$$\frac{1 - \exp(2\,\mu\, b/\sigma^2)}{\exp(-2\,\mu\, a/\sigma^2) - \exp(2\mu b/\sigma^2)}$$

and

$$\frac{\exp(-2\,\mu\,/\sigma^2) - 1}{\exp(-2\,\mu\, a/\sigma^2) - \exp(2\,\mu\, b/\sigma^2)},$$

respectively. If b is set equal to the initial value, the second of these represents the probability of extinction. It is difficult to specify appropriate values for σ. For example, $\sigma = 100$ implies that with 95% probability the actual increase might vary from 200 above to 200 below the mean. Such variations are not unreasonable in the Arctic environment. We do not know if they are this large or not but catastrophic mortality due to ice conditions has been recorded (Sleptsov 1948, as cited by Tomilin 1957, in text but no citation given). We have assumed that stresses are independent events from year to year. To apply this we consider the female population which, in a total of 2,000, will number about 1,000. Extinction clearly occurs if this component falls to zero. We arbitrarily have assumed that if the female population reaches 2,000, the population is safe from extinction. If a larger "safe" upper limit is chosen, then the probabilities of extinction will be greater. It should be noted that the level of 2,000 females (or any other upper limit) is not an absorbing barrier in the sense that zero, the lower limit, is. However, to simplify the model, we have chosen a range within which it is reasonable to assume average growth is approximately constant—over a wider range the growth parameter must change. Because we have assumed constant μ (average increment), the probabilities of a population becoming extinct with 1,000 females are easily computed from the given formula for various levels of average annual increase and various levels of environmental stress as expressed by standard deviation.

RESULTS

Risk Analysis

The effect of the level of exploitation on the risk of extinction is shown in Table 2. A catch of 10 whales shifts the average increase downward by that amount; i.e., one moves one column to the left in the table. A continuing kill of 30 whales shifts the probabilities three columns to the left. Thus, if present net recruitment were 50 whales and the environmental perturbation were represented by $\sigma = 141.4$, the probability of extinction according to this model would be increased from 0.01 to 0.12 with a continuing 30 whale kill.

Initial Stock Size

It can be seen that the initial stock estimates are little affected by the estimates or assumptions of

TABLE 2.—Probabilities of extinction for stochastic process with normally distributed independent additive increments.

Stress variability σ	Average annual increase, μ					
	10	20	30	40	50	60
0.7	0.02	—	—	—	—	—
100	.12	0.02	0.002	—	—	—
141.4	.27	.12	.05	0.02	0.01	0.002
173.2	.34	.21	.12	.06	.03	.02

the current (1978) stock level given the same values of the other parameters $(r - M)_{max}$, M, and τ (Figure 2, Table 3). Table 4 shows the initial stock size estimates from Table 3 (1978 stock level of 2,700) reexpressed as deviations from row and column medians. The magnitude and direction of changes in the estimates as a function of the different parameter combinations indicate that in-

FIGURE 2.—Population back projections (where $M = 0.06$, Lag = 5 yr, $(r - M)_{max} = 0.03$) which would theoretically result in current stock sizes of 900, 1,500, and 2,700 bowhead whales according to the model (see text).

TABLE 3.—Results of iterative solution of Equation (3). Initial stock size estimates (in thousands) for various values of vital parameters (M, lag time, and maximum net recruitment rate) and 1978 stock level.

		1978 stock level of 900			1978 stock level of 1,500			1978 stock level of 2,100			1978 stock level of 2,700		
		$(r - M)_{max}$			$(r - M)_{max}$			$(r - M)_{max}$			$(r - M)_{max}$		
M	Lag time (yr)	0.01	0.03	0.05	0.01	0.03	0.05	0.01	0.03	0.05	0.01	0.03	0.05
0.04	1	25.67	21.95	19.64	25.91	21.98	19.64	26.15	22.02	19.65	26.40	22.05	19.65
.06		25.15	21.90	19.23	25.38	21.90	19.23	25.63	21.56	19.24	25.88	21.60	19.24
.08		24.62	21.41	18.82	24.86	21.44	18.82	25.10	21.10	18.83	25.35	21.14	18.83
.04	3	24.01	20.72	18.68	24.27	20.76	18.69	24.54	20.81	18.69	24.81	20.86	18.70
.06		22.77	19.69	17.78	23.04	19.74	17.79	23.31	19.80	17.80	23.60	19.85	17.81
.08		21.61	18.73	16.93	21.89	18.78	16.94	22.17	18.64	16.96	22.47	18.90	16.97
.04	5	22.56	19.63	17.83	22.84	19.69	17.84	23.13	19.76	17.86	23.43	19.82	17.87
.06		20.82	18.19	16.56	21.12	18.26	16.58	21.43	18.33	16.59	21.74	18.41	16.61
.08		19.29	16.90	15.42	19.60	16.98	15.44	19.92	17.11	15.57	20.25	17.16	15.49
.04	7	21.29	18.67	17.07	21.59	18.75	17.09	21.90	18.83	17.11	22.22	18.91	17.14
.06		19.21	16.92	15.52	19.53	17.02	15.55	19.86	17.11	15.57	20.20	17.21	15.61
.08		17.44	15.43	14.18	17.78	15.54	14.22	18.13	15.65	14.25	18.49	15.77	14.29

TABLE 4.—Reexpressed stock sizes of Table 3 (1978 stock level of 2,700).

		Row values minus medians				Column values minus medians		
		$(r - M)_{max}$				$(r - M)_{max}$		
M	Lag time (yr)	0.01	0.03	0.05	Median	0.01	0.03	0.05
0.04	1	4.35	0.00	−2.40	22.05	0.52	0.45	0.41
.06		4.28	.00	−2.36	21.60	.00	00	.00
.08		4.21	.00	−2.31	21.14	− .53	− .46	−0.41
					Median	25.88	21.60	19.24
.04	3	3.95	.00	−2.16	20.86	1.21	1.01	0.89
.06		3.75	.00	−2.04	19.85	.00	.00	.00
.08		3.57	.00	−1.93	18.90	−1.13	− .95	− .84
					Median	23.60	19.85	17.81
.04	5	3.61	.00	−1.95	19.82	1.69	1.41	1.26
.06		3.33	.00	−1.80	18.41	.00	.00	.00
.08		3.09	.00	−1.67	17.16	−1.49	−1.25	−1.12
					Median	21.74	18.41	16.61
.04	7	3.31	.00	−1.77	18.91	2.02	1.70	1.53
06		2.99	.00	−1.60	17.21	.00	00	.00
.08		2.72	.00	−1.48	15.77	−1.71	−1.44	−1.32
					Median	20.20	17.21	15.61

creasing values of M, lag time, and maximum net recruitment tend to decrease the estimate of initial stock size.

Vital Parameters

The natural mortality rate has somewhat less of an effect on initial stock estimates than does the maximum net recruitment rate. This can be seen from Table 4 where initial stock estimates have been reexpressed as deviations from row and column medians. As noted above, net recruitment rates >0.05 often did not result in convergence of the iterative procedure. In general, convergence occurred only if fractions of animals were allowed in Equation (2). If only integer numbers were used, it was virtually impossible to arrive at a prescribed stock level in 1978 from a given stock level. This is because the time series consists of over 100 yr, and rounding-off errors become critical if the convergence criterion is too stringent. We assumed convergence if the difference between two successive initial stock estimates was <0.1.

Maximum net recruitment rate and lag time are the most sensitive of the parameters we use in the model and natural mortality rate the least. We have used all combinations of the range of values of the parameters, although we recognize that certain combinations are likely to be unreasonable (for instance, a lag time of 1 yr with a maximum net recruitment rate of 0.01 is unlikely and therefore the initial stock size is unreasonable for these parameter values).

Bockstoce[10] examined a sample of maritime newspapers and logbooks of whaling voyages and estimated that 22,111 bowheads were killed by pelagic whalers in the "commercial" fishery between 1848 and 1915. Mitchell (footnote 4) estimated 27,714 whales killed in both the "commercial" and the "aboriginal" fisheries during this period. Initial stock size estimates using the data in Bockstoce (footnote 10) for 1848-1915 and our Table 1 for 1916-77 are about 15% lower than the results given in Table 3.

Recovery Times

Using the basic model of Equation (2) and assuming that the maximum net recruitment rate applies in the current season (assuming a population of 1,500 and 2,700 animals), the time required to recover to one-half of an initial stock level of 18,000 was calculated for various parameter values. These are presented in Table 5 as a ratio of time to recover to 9,000 with a constant kill (5, 10, 15, 20, 25, and 30 animals) compared with the time to recover without a kill.

If the current stock level were 1,500 animals and the maximum net recruitment rate was 0.05, M = 0.04, time lag 3 yr, the stock would take 58 yr to recover to a level of 9,000 with no kill vs. 75 yr with a kill of 30/year. These numbers are increased to 94 and 153 yr, when the maximum net recruitment rate is only 0.03 (other parameters unchanged).

DISCUSSION

We believe our model is useful but not fully adequate. We have reservations about the data used, limitations of the model, and aspects of the fishery that we did not have time or data to adequately address.

Limitations of the Data

The commercial catch data are based mainly on extrapolations of a consistent number of whales caught per ship. The statistics for the number of vessels operating in the bowhead fishery component of the North Pacific Ocean are also subject to

[10]Bockstoce, J. 1978. A preliminary estimate of the reduction of the western Arctic bowhead whale (*Balaena mysticetus*) population by the pelagic whaling industry: 1848-1915. Report submitted to U.S. Marine Mammal Commission, Washington, D.C. Available U.S. Dep. Commer., Natl. Tech. Inf. Serv., Springfield, VA 22161, as PB-286-797.

TABLE 5.—Estimated recovery times for Bering Sea bowhead whale stock. Recovery time is that calculated with the parameters indicated, assuming zero kill. The relative increases in recovery time that occur with various levels of constant kill are tabulated in the last six columns.

Assumed current stock level	Lag time used in model	$(r - M)_{max}$	M	Recovery time (yr) to 9,000	Annual kill					
					5	10	15	20	25	30
1,500	3	0.01	0.04	273	1.22	1.63	[1]	—	—	—
			08	302	1.21	1.58	—	—	—	—
		.03	04	94	1.06	1.14	1.22	1.33	1.46	1.63
			08	104	1.06	1.13	1.20	1.30	1.41	1.57
		.05	04	58	1.05	1.09	1.12	1.17	1.22	1.29
			08	64	1.03	1.06	1.11	1.16	1.20	1.27
	7	.01	04	315	1.22	1.63	—	—	—	—
			08	381	1.21	1.58	—	—	—	—
		.03	04	110	1.06	1.14	1.22	1.33	1.45	1.63
			08	131	1.06	1.13	1.21	1.31	1.43	1.59
		.05	04	69	1.03	1.07	1.12	1.16	1.22	1.28
			08	81	1.04	1.07	1.12	1.16	1.21	1.27
2,700	3	.01	04	197	1.16	1.39	1.75	2.45	—	—
			08	218	1.15	1.36	1.69	2.28	—	—
		.03	04	68	1.04	1.09	1.15	1.22	1.29	1.38
			08	74	1.05	1.09	1.16	1.22	1.28	1.36
		.05	04	42	1.02	1.05	1.07	1.12	1.14	1.19
			08	46	1.02	1.04	1.09	1.11	1.13	1.17
	7	.01	04	226	1.16	1.39	1.74	2.45	—	—
			08	274	1.15	1.36	1.69	2.28	—	—
		.03	04	78	1.05	1.10	1.15	1.22	1.29	1.38
			08	93	1.04	1.10	1.15	1.22	1.29	1.37
		.05	04	48	1.04	1.06	1.08	1.13	1.17	1.21
			08	57	1.04	1.05	1.09	1.12	1.16	1.19

[1]Stock goes to zero.

much interpretation (Mitchell footnote 4), but at least the extrapolations will approximate true trends.

The aboriginal catch data for some years may represent only the minimum landed catch. The pre-1960 aboriginal catch fluctuates from 0 to 47 (1908) per annum, where presently known. From 1978 back to 1854 there are many years for which no data were recorded or obtainable. Also, for many years for which data are available, the numbers given may not represent the true total landed catch. In our analysis, these unrecorded kills have implications only for the data from 1908 or 1912, near the end of the commercial pelagic fishery when the aboriginal catch begin to represent the majority of the total catch. However, during the much earlier period of high commercial catches, the aboriginal catch composed a small percentage of the total (5% or less of the pelagic catch at its highest). Thus any analysis of recovery patterns dependent upon the post-1900 data is entirely dependent upon the completeness of the aboriginal catch. Since few contemporary written records have been kept and continued library research yields new figures for given years, the aboriginal catch must be regarded as minimum and provisional.

Limitations of the Model

All models with published results previously used on whale populations have been applied to odontocetes, balaenopterids, or eschrichtiids, but not to balaenids. Because we are dealing with a separate zoological family (much older than the balaenopterids and apparently different in many behavioral features), caution should be used when applying balaenopterid vital parameter values, by analogy, to the balaenid model. No other reasonable estimates are available, however.

Although the model (Equation 2) used to estimate initial abundance is relatively simple, it does account for fishing and natural mortality and recruitment as a function of the time-lagged population size. It is quite possible, though, given the 130 yr we are considering, that the natural mortality rate has changed. Such a change, if it has occurred, probably would have had a relatively small effect on the initial stock estimates. We have also not considered the effect of a differential sex ratio in the large pelagic catches, which could have resulted in the 1912 population consisting of (in the worst possible cases) mostly males, mostly old females of low fertility, or young animals of either sex.

Although Figure 2 shows a minimum population size occurring around 1912, we have not calculated the minimum size the population might have declined to, for the following reasons: assumptions that the population was much smaller then (and has appreciably recovered) cannot be proven, and represent only one alternative explanation of the

history of the fishery and of the population since the early 1900's. For example, we do not know how the 1912 population was structured. If, as seems likely with high prices for baleen, selection mainly for large animals with long baleen occurred near the end of the fishery, then the remnant population might have comprised a large proportion of young animals. The 1977 population might represent a considerable proportion of this 1912 population, now old, and we would know little about net recruitment or failure thereof.

The most difficult parameter to estimate in any whale population is the recruitment rate. In the absence of better knowledge, we have used a simple linear model and specified a range of maximum net recruitment rates. Given that the recruitment rate function varies between some maximum value at stock level near zero and M at P_0, the shape of the curve has less effect than the value of $(r-M)_{max}$. During the early history of the fishery, catches exceeded recruitment, and during the last half-century the stock was at a relatively low level. Thus, the recruitment rate was close to its maximum and varied little. A further study could consider the effect of a dome-shaped recruitment curve.

Given our results, it appears likely that stock size between 1910 and 1978 was probably <10% of the initial stock level. According to most classical models used with baleen whale populations, the net recruitment should have been near its maximum for about the last 60 yr. Because the population does not appear to have grown substantially since then, either the recruitment rate has been low or the kills have been higher than currently estimated. It is also possible that the catches during the last half-century represent survivors of the then young animals.

Aspects of the Fishery

We may have to consider very low net recruitment rates because the changing nature of the fishery suggests that, as the worst case, the whalers efficiently decimated a structured population successively over its geographic range. The argument is as follows: females with calves migrate farther north (later, in the migration stream) and also inhabit ice fields. They might not have been as available to the early fishery, 1850-ca. 1870's, which used sailing vessels at the ice edge and which was mainly a midsummer to late season fishery. The greatest removals were during this time and for a short period. Subsequently, with the development of steam whaling, overwintering of the fleet became possible, and heavy fishing occurred in the ice fields at all times. The fishing season was effectively increased in length between the 1880's and 1910's. (Even if the population were not so structured by sex or age, the present spring and summer distribution is confined to a much smaller area compared with the data of Townsend (1935).)

Due to the unique geography, stratification, and timing of this fishery, the possibility exists that once the stock is fished to some low level, recruitment failure could occur and that net recruitment since about 1900 could indeed be as low as 0.01, the minimum figure used in our calculations.

Any subsequent analysis of annual catch and effort data (e.g., including number of vessels, etc.) should consider changing technology. The fishery changed radically from one of a sailing vessel-ice edge-early season fishery to a steam vessel-ice pack-nearly year round fishery. The best measure of change in effort between sailing and steam vessels to catch the same number of whales might be the monthly duration of the respective voyages.

ACKNOWLEDGMENTS

We thank M. F. Tillman, D. W. Rice, and V. M. Kozicki for critically reading the manuscript. G. Ferrand drafted Figure 1. J. M. Breiwick acknowledges support under contract MM8AC007 from the U.S. Marine Mammal Commission.

LITERATURE CITED

ALLEN, K. R.
1966. Some methods for estimating exploited populations. J. Fish. Res. Board Can. 23:1553-1574.

BRAHAM, H., B. KROGMAN, S. LEATHERWOOD, W. MARQUETTE, D. RUGH, M. TILLMAN, J. JOHNSON, AND G. CARROLL.
1979. Preliminary report of the 1978 spring bowhead whale research program results. Rep. Int. Whaling Comm. 29:291-306.

CLARK, A. H.
1887. Part XV. The whale fishery. 1.—History and present condition of the fishery. *In* G. B. Goode and a staff of associates, The fisheries and fishery industries of the United States, Sect. V, Vol. 2, p. 3-218. Gov. Print. Off., Wash., D.C.

COOK, J. A.
1926. Pursuing the whale. A quarter-century of whaling in the Arctic. Houghton Mifflin Co., Boston, 344 p.

COX, D. R., AND H. D. MILLER.
1965. The theory of stochastic processes. Wiley, N.Y., 398 p.

DOI, T., S. OHSUMI, AND T. NEMOTO.
1967. Population assessment of sei whales in the Antarctic. Nor. Hvalfangst-Tidende. 56:25-41.

DURHAM, F. E.
1979. The catch of bowhead whales (*Balaena mysticetus*) by Eskimos, with emphasis on the western Arctic. Contrib. Sci., Nat. Hist. Mus. Los Ang. Cty. 314, 14 p.

INTERNATIONAL WHALING COMMISSION.
1971. Report of the special meeting on Antarctic fin whale stock assessment. Rep. Int. Whaling Comm. 21:34-39.
1978. Report of the scientific committee. Rep. Int. Whaling Comm. 28:38-129.

MAHER, W. J., AND N. J. WILIMOVSKY.
1963. Annual catch of bowhead whales by Eskimos at Point Barrow, Alaska, 1928-1960. J. Mammal. 44:16-20.

MARQUETTE, W. M.
1976. Bowhead whale field studies in Alaska, 1975. Mar. Fish. Rev. 38(8):9-17.

RICE, D. W.
1974. Whales and whale research in the eastern North Pacific. *In* W. E. Schevill (editor), The whale problem: a status report, p. 170-195. Harv. Univ. Press, Camb., Mass.

SERGEANT, D. E., AND W. HOEK.
1974. Seasonal distribution of bowhead and white whales in the eastern Beaufort Sea. *In* J. C. Reed and J. E. Sater (editors), The coast and shelf of the Beaufort Sea, p. 705-719. Arctic Inst. North Am., Arlington, Va.

TOMILIN, A. G.
1957. Zveri SSSR i prilezhashchikh stran (Mammals of the U.S.S.R. and adjacent countries). Kitoobraznye (Cetacea). Vol. IX. Izd. Akad. Nauk SSSR, Moskva, 756 p. (Translated by Isr. Program Sci. Transl., 1967, 717 p.; available Natl. Tech. Inf. Serv., Springfield, Va., as TT 65-50086.)

TOWNSEND, C. H.
1935. The distribution of certain whales as shown by logbook records of American whaleships. Zoologica (N.Y.) 19, 50 p.

SPAWNING BIOMASS AND EARLY LIFE OF NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, IN THE NORTHERN SUBPOPULATION OFF OREGON AND WASHINGTON

SALLY L. RICHARDSON[1]

ABSTRACT

A major spawning center for the northern subpopulation of northern anchovy, *Engraulis mordax*, is documented off the Oregon-Washington coast beyond the continental shelf, based on collections of planktonic eggs in July 1975 and July 1976. Biomass estimates of northern anchovy in this spawning concentration ranged from 262,506 to 769,511 metric tons in 1975 and 144,654 to 1,005,263 metric tons in 1976, based on egg and larva surveys. Spawning biomass was estimated to be 800,000 metric tons in 1977, based on an acoustic survey of adults. The most probable biomass may be more than 100,000 but less than 1,000,000 metric tons. Potential yield estimates ranged from 86,792 to 633,316 metric tons, but realizable yields may be considerably lower if management strategies applied to northern anchovy in the central subpopulation are implemented for the northern subpopulation.

Spawning appears to be associated with waters of the Columbia River plume which may provide favorable conditions, in terms of stability and productivity, for survival of first feeding northern anchovy larvae. Evidence of larval transport south away from the spawning center leads to questions about return mechanisms to explain the occurrence of juveniles in Oregon bays and rivers later in the season. Additional spawning centers within the range of the northern subpopulation have not been documented although some evidence from the literature indicates another spawning center may occur in the Strait of Georgia, British Columbia, around the Fraser River plume.

Conditions related to spawning differ between the northern and central subpopulations. Off Oregon, spawning occurs from mid-June to mid-August, when current flow to the south is at a maximum, water temperatures are reaching maximum levels for the year, coastal upwelling is at a maximum, and day length is at or near maximum duration. Off California, peak spawning occurs from January through April when southward current flow is minimal, water temperatures are reaching minimal levels for the year, upwelling is minimal, and day length is at minimum duration. These factors are indicative of some degree of reproductive isolation as well as differing reproductive strategies between the two subpopulations.

The northern anchovy, *Engraulis mordax* Girard, is an abundant pelagic schooling fish that occurs along the west coast of North America from Cape San Lucas, Baja California, to the Queen Charlotte Islands, British Columbia (Miller and Lea 1972; Hart 1973). It is the object of an expanding fishery off central and southern California and Baja California where about 204,000 metric tons (t) were harvested in 1975, mainly for fish meal (Pacific Fishery Management Council[2]). In the northern part of its range it is utilized only to a small degree as bait by local fishermen although its potential as a harvestable resource has been suggested (Pruter 1966, 1972). Reports of dense schools off the Oregon and Washington coasts indicate northern anchovy biomass may be substantial (Pruter 1966, 1972). Estimates of an annual consumption of 28,000 t of northern anchovy by four species of marine birds off the Oregon coast (Wiens and Scott 1975) further indicates sizeable biomass.

In the absence of a fishery, biomass estimates are unavailable for northern anchovy north of California. We know that in the 1940's northern anchovy in ocean waters adjacent to the Columbia River supported a live bait fishery for albacore tuna (Pruter 1966, 1972). Reported commercial landings of northern anchovy in Washington in 1947-49 ranged from 20 to 182 t annually and were 28 and 76 t in Oregon in 1948 and 1953 (Pruter 1966). A small purse seine fishery for canning once existed around southern British Columbia where harvests ranged from 64 to 6,201 t annually between 1939 and 1947 (Roach and Harrison 1948; Pike 1951).

[1]School of Oceanography, Oregon State University, Corvallis, Oreg.; present address: Gulf Coast Research Laboratory, East Beach Drive, Ocean Springs, MS 39564.

[2]Pacific Fishery Management Council. 1978. Northern anchovy fishery management plan. U.S. Dep. Commer., NOAA Federal Register 43(141) Book 2:31651-31783.

Manuscript accepted March 1980.
FISHERY BULLETIN: VOL. 78, NO. 4, 1981.

Because of the relatively unfished state of northern anchovy off Oregon and Washington, the lack of biomass estimates, and the potential for fishery development, this study was undertaken to define spawning centers and provide the first preliminary estimates of spawning biomass within such defined spawning centers by means of ichthyoplankton survey. Additional information on adult school distributions and another independent estimate of biomass were obtained by acoustic survey (Smith[3]). Ecological data on the early life of these northern occurring fish were also examined. Aspects of adult life history, particularly reproduction, are presented in a separate paper (Laroche and Richardson 1981).

THE NORTHERN SUBPOPULATION

Northern anchovy occurring north of Cape Mendicino, Calif., compose the northern subpopulation of *E. mordax*, one of three subpopulations (Figure 1) distinguished on the basis of meristic counts (McHugh 1951) and electrophoretic separation of blood serum protein (Vrooman and Paloma[4]). The central subpopulation occurs primarily off southern California and northern Baja California and the southern subpopulation is off central and southern Baja California. A separate subspecies, *E. mordax nanus*, has also been described from San Francisco Bay (Hubbs 1925).

Compared with the central and southern subpopulations, relatively little detailed information is available on spawning and early life history of northern anchovy in the northern subpopulation. Off California and Baja California spawning seasons and locations are well defined (e.g., Ahlstrom 1966, 1967; Baxter 1967; Kramer and Ahlstrom 1968), eggs and larvae have been illustrated (Bolin 1936; Ahlstrom 1956, 1965; Kramer and Ahlstrom 1968), and spawning biomass has been estimated on the basis of larva survey (e.g., Pacific Fishery Management Council footnote 2).

For the northern subpopulation, information on spawning and early life history had to be pieced together from a number of sources to provide the background for the present study. Based on monthly plankton collections of larvae off Oregon

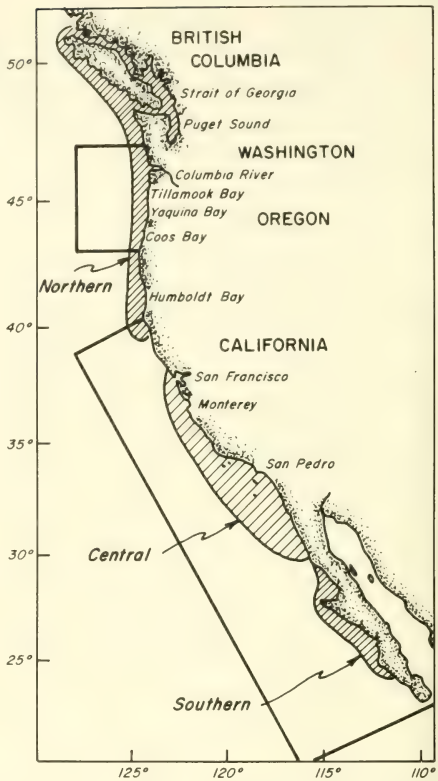


FIGURE 1.—Geographic ranges (hatched) of the three subpopulations (northern, central, southern) of *Engraulis mordax* (modified from Smith and Lasker in press). Rectangular area outlined off Oregon and Washington shows ichthyoplankton survey grid boundaries for this study. Rectangular area outlined off California and Baja California shows approximate boundaries of the principal portion of the CalCOFI survey grid (after Kramer et al. 1972).

(Richardson 1973, see footnote 5; Richardson and Pearcy 1977) and maturity studies involving measurements of ova diameters from ovaries of fish collected off British Columbia (Pike 1951), the spawning season is short, lasting from about mid-June to mid-August. Based on available catch records (Williamson 1929 [in Pike 1951]; Pike 1951;

[3]P. E. Smith, Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun. March 1978.

[4]Vrooman, A. M., and P. A. Paloma. 1975. Subpopulations of northern anchovy, *Engraulis mordax* Girard. NOAA NMFS Southwest Fish. Cent., Admin. Rep. No. LJ-75-62, 10 p.

[5]Richardson, S. L. 1977. Larval fishes in ocean waters off Yaquina Bay Oregon: abundance, distribution, and seasonality January 1971 to August 1972. Oreg. State Univ. Sea Grant Coll. Prog. Publ. No. ORESU-T-77-003, 73 p.

Parsons et al. 1970; Eldridge and Bryan 1972; Blackburn 1973; Richardson 1973, footnote 5, unpubl. data; Pearcy and Myers 1974; Laroche 1976; Misitano 1977; Richardson and Pearcy 1977; Waldvogel 1977; Robinson[6]; Cummings and Schwartz[7]; Forsberg et al.[8]) spawning locations have not been well defined and data are somewhat contradictory. Before the present study, running ripe adults had never been collected. Two nearly ripe females were taken in coastal waters around British Columbia; one ripening female was taken in Tillamook Bay in northern Oregon; and large numbers of ripening adults had been found in Humboldt Bay in northern California (Figure 1). Interestingly, the ripening fish in Humboldt Bay leave in June or July and return again in fall in a spent condition. Planktonic northern anchovy eggs had been reported only from certain inlets of Vancouver, British Columbia, in Puget Sound, Wash., off the Columbia River mouth, and in Yaquina Bay, Oreg. Small (<10 mm) planktonic larvae had been rarely taken in areas where ripening adults or planktonic eggs had been found. Small numbers of these larvae had been reported only from Yaquina Bay and Humboldt Bay. Large concentrations of small larvae had been reported only from ocean waters off Oregon. Larvae ≥10 mm had been taken in small numbers in the Strait of Georgia, British Columbia, inside the mouth of the Columbia River, in Yaquina Bay, and in Humboldt Bay. As with small larvae, large concentrations had been found only off the Oregon coast. Juveniles ≥35 mm had been taken in ocean waters off Oregon as well as in the Strait of Georgia, British Columbia; Puget Sound, Wash., inside the Columbia River mouth; in Tillamook Bay, Yaquina Bay, and Coos Bay, Oreg.; and in Humboldt Bay, Calif. Juveniles taken offshore were usually <50 mm while most of those in bays and sounds were >50 mm.

These data, and particularly the earlier study by Richardson (1973), indicated the possible existence of a spawning concentration of northern anchovy within the northern subpopulation located off the Oregon-Washington coast. Richardson suggested spawning might be associated with the Columbia River plume. The present study was designed to test that hypothesis and to estimate the biomass of spawning adults located therein.

METHODS

Field Procedures

Standard ichthyoplankton surveys (Smith and Richardson 1977) were conducted off the Oregon-Washington coast in the region outlined in Figure 1. This survey area was designed to border at least the inner bounds of the Columbia River plume. Cruises were conducted at the presumed time of peak spawning in mid-July: 10-18 July 1975 and 7-15 July 1976.

A grid of 70 stations along seven east-west transects (Figure 2) was sampled. Stations ex-

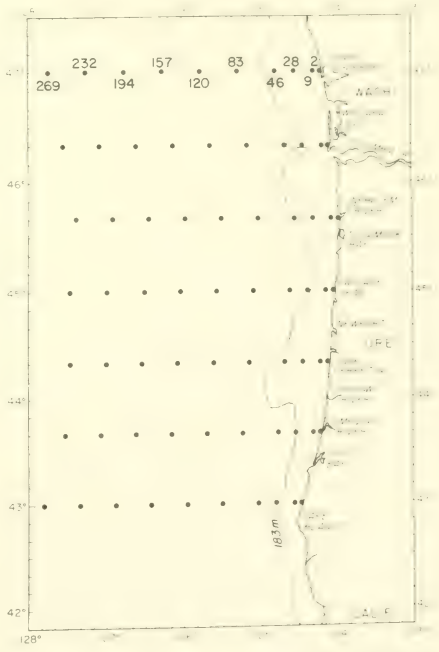


FIGURE 2.—Ichthyoplankton survey grid with 70 cm bongo net sampling stations occupied in July 1975 and July 1976 off Oregon and Washington. Numbers on upper transect represent kilometers from the coast and apply to all seven transects.

[6]Robinson, D. G. 1969. Data record. Number, size composition, weight and food of larval and juvenile fish caught with a two-boat surface trawl in the Strait of Georgia July 4-6, 1967. Fish. Res. Board Can., Manuscr. Rep. Ser. No. 1012, 71 p.

[7]Cummings, E., and E. Schwartz. 1971. Fish in Coos Bay, Oregon, with comments on distribution, temperature, and salinity of the estuary. Oreg. Fish. Comm., Res. Div., Coastal Rivers Invest. Inf. Rep. 70-11, 22 p.

[8]Forsberg, B. O., J. A. Johnson, and S. M. Klug. 1976. The identification, distribution, and notes on food habits of fish and shellfish in Tillamook Bay, Oregon. Oreg. Dep. Fish Wildl., Res. Sect., Fed. Aid Prog. Rep.: Fish., Feb. 1974-June 1976, 117 p.

tended from 2 to 269 km offshore and covered a north-south distance of 450 km. Transects were 74 km apart and stations on a transect were 46 km apart except the most inshore stations which were closer together. The grid covered an area of 120,150 km^2.

Oblique 70 cm bongo net tows were made at each station from 150 m (or just above the bottom) to the surface. Vessel speed was 2-3 knots and retrieval speed was 20 m/min. The bongos were fitted with 0.333 and 0.571 mm mesh Nitex[9] nets, TSK flowmeters and a time-depth recorder. Stations were occupied when the ship arrived, day or night. Samples were preserved in 10% buffered Formalin.

Temperature, salinity, and chlorophyll were monitored at 3 m depth every 9 km along each transect using a flow-through fluorimeter system (AMINCO Fluro-colorimeter). At each bongo station a bathythermograph cast was made to 140 m depth (or 5 m above the bottom) and a surface bucket temperature was recorded. During the July 1976 cruise, surface drifters, consisting of a labelled plastic tag made buoyant with Styrofoam, were released to provide information on surface water movement. Fourteen drifters were dropped at each bongo station except on the southernmost transect (lat. 43°00′ N) where only 10 were released at the 120 km station and none at the 157, 194, 232, and 269 km stations.

Between 18 and 25 July 1977 an acoustic survey was conducted cooperatively by the National Marine Fisheries Service (NMFS) in the same area as the previous ichthyoplankton surveys (Smith[10]). The same seven transects plus an eighth transect to the south along lat. 42°20′ N were surveyed acoustically during daylight using the methods of Smith (1970). Distance covered on each line extended from the 91 m depth contour westward 167 km. In addition to the acoustic work, temperature and salinity at 3 m depth were monitored every 9 km using a flow-through salinograph, and expendable bathythermographs were cast every 9 km on every other transect. Following a day's sonar run, nighttime surface trawls were made with a 40 m modified Cobb pelagic trawl (Smith footnote 10) on the latter half of the sonar track in areas of biological aggregations identified and measured by sonar. Standard oblique 60 cm bongo tows (Smith and Richardson 1977) were made at each trawl station from 70 m to the surface. Samples were processed at sea using CalCOFI (California Cooperative Oceanic Fisheries Investigations) techniques (Kramer et al. 1972) except that the 0.333 mm mesh samples were preserved in ethyl alcohol for special studies (Methot[11]).

Laboratory Procedures

Plankton volumes for each 0.333 mm mesh bongo sample from the 1975 and 1976 cruises were determined by displacement (Kramer et al. 1972), and northern anchovy eggs and all fish larvae were sorted. Northern anchovy eggs were enumerated. Measurements of long and short axes of eggs were made on selected samples using an ocular micrometer in a stereomicroscope. Northern anchovy larvae were identified, enumerated, and measured in 0.5 mm size classes using a plastic rule beneath a glass slide. The 0.333 mm mesh bongo samples only from the 1977 cruise were processed by personnel from Scripps Institution of Oceanography and the NMFS Southwest Fisheries Center according to techniques described by Kramer et al. (1972). Numbers of eggs and larvae in each sample were standardized to the number under 10 m^2 sea surface (Smith and Richardson 1977):

$$C_i = 10\,(a_i^{-1} b_i^{-1} c_i d_i) \qquad (1)$$

where C_i = number of eggs or larvae beneath 10 m^2 sea surface at station i
a = mouth area of the bongo net used at station i in square meters
b = length of tow path in meters estimated from a calibrated flowmeter at station i
c = number of eggs or larvae in the ith sample
d = maximum depth of tow in meters.

Egg and Larva Census Estimates

Census estimates (i.e., estimates of the total number of northern anchovy eggs and larvae in

[9]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[10]Smith, P.E. 1977. Cruise report, R/V *David Starr Jordan*, 7705(111), Mordax North, Leg A, 13-27 July 1977. Rep. dated 5 December 1977. On file at National Marine Fisheries Service Southwest Fisheries Center, P.O. Box 271, La Jolla, CA 92038.

[11]R. D. Methot, Scripps Institution of Oceanography, Graduate Department, La Jolla, CA 92093, pers. commun. July 1977.

the area represented by the survey grid during each cruise in 1975 and 1976) were determined by two methods, the Sette and Ahlstrom Census and the Smith Census. The Sette and Ahlstrom Census was the polygon method of Sette and Ahlstrom (1948) in which the number of individuals under 10 m^2 sea surface at each station was weighted by the area represented by the station. These areas are polygons formed "by constructing perpendicular bisectors of lines drawn from the station to each of all surrounding stations" (Sette and Ahlstrom 1948). The census estimate is then:

$$C_k = 10 \sum_{i=1}^{n} A_s (a_i^{-1} b_i^{-1} c_i d_i) \qquad (2)$$

where C_k = estimate of abundance of eggs or larvae during cruise k
A_s = area of a polygon constructed of perpendicular bisectors of lines between station i and all adjacent stations
n = number of stations.

Polygon areas, determined by planimeter, ranged from 0.38 to 2.89 $\times 10^9$ m^2 but were $>2.00 \times 10^9$ m^2 for all stations 46 km or more from the coast.

The Smith Census was the "regional census estimate" of Smith (1972):

$$C_{kr} = 10 A_r n^{-1} \sum_{i=1}^{n} (a_i^{-1} b_i^{-1} c_i d_i) \qquad (3)$$

where C_{kr} = estimate of abundance of eggs or larvae in region r during cruise k
A_r = area of region r in numbers of 10 m^2 areas (in my study,

$$10 A_r = \sum_{i=1}^{n} A_s = 148.81 \times 10^9 \text{ m}^2).$$

The Smith Census method can be less tedious than the Sette and Ahlstrom Census method if the area represented by the survey can be determined in a gross manner, i.e., without planimetry. Values of the Smith Census in my study were always lower than those of the Sette and Ahlstrom Census. The Smith Census was computed here primarily to allow for comparison with CalCOFI data (Smith 1972; Pacific Fisheries Management Council footnote 2).

Spawning Biomass Estimates

Four methods were used to estimate spawning biomass, three based on egg census estimates (Sette and Ahlstrom Egg Method, Simpson Egg Method, Saville Egg Method) and one based on larva census estimates (Smith Larva Method). The use of three egg methods generally follows the approach of Houde (1977) in estimating spawning biomass of round herring, *Etrumeus teres*. Because the shape of the egg production curve throughout the spawning season is unknown for northern anchovy, the use of these three egg methods takes into account the range of possibilities (discussed below) for comparative purposes.

All three egg methods ultimately use the same formula (Saville 1964) to estimate spawning biomass:

$$B = \frac{E_s}{KF} \qquad (4)$$

where B = biomass of spawning adults
E_s = total number of eggs spawned during a season, i.e., seasonal egg production. (This estimate varies according to the egg method used as described below.)
K = the proportion of spawning adults that are females. [In this paper the overall sex ratio of *E. mordax* is assumed to be 1:1 following Smith (1972) and Klingbiel (1978).]
F = mean fecundity, i.e., the number of eggs produced per gram of female per spawning season. [The mean fecundity of *E. mordax* in the northern subpopulation off Oregon is estimated to be 720 ova/g total weight female (Laroche and Richardson 1981).]

The number of eggs spawned in a season (E_s) was estimated by three methods, each using the two egg census estimates described above.

The Sette and Ahlstrom Egg Method of estimating seasonal egg production (E_s) follows the approach of Sette and Ahlstrom (1948).

$$E_s = \sum_{i=1}^{N} \frac{C_k D_i}{t_i} \quad \text{or} \quad \sum_{i=1}^{N} \frac{C_{kr} D_i}{t_i} \qquad (5)$$

where N = number of cruises in a season
D_i = number of days represented by cruise i. [Sette and Ahlstrom (1948) defined this to be the days included in the cruise plus one-half the days since the previous cruise and one-half the days to the next cruise; in this study only one cruise was made during the spawning season and the number of days represented by the cruise was taken to be the entire spawning season. Duration of the spawning season for *E. mordax* off the Oregon-Washington coast was estimated from monthly or bimonthly collections of larvae taken off Oregon in 1969, 1971, and 1972 (Richardson 1973, footnote 5, unpubl. data; Richardson and Pearcy 1977). The earliest that northern anchovy larvae were taken in those years was 19 June and the latest that small larvae (<10 mm) were collected was 10 August. Peak abundance, >100/10 m^2 or >1,000/1,000 m^3 at a station, occurred only between 21 July and 6 August. The spawning season was estimated to last approximately from 15 June to 15 August, or 62 days.]
t_i = the time in days from spawning to hatching of the egg determined from the equation given by Zweifel and Lasker (1976) for incubation times for northern anchovy:

$$I_T = I_0 \exp [m(1 - \exp(-\beta T))] \quad (6)$$

where $I_0 = 1861$
$m = -5.4572$
$\beta = 0.0626$
T = the mean temperature at 3 m depth at stations where northern anchovy eggs were taken, 15.18° C in 1975 and 16.09° C in 1976.

The Sette and Ahlstrom Egg Method assumes a constant egg production throughout the spawning season.

The Simpson Egg Method of estimating the number of eggs spawned in a season (E_s) was that given by Simpson (1959) as modified by Houde (1977). The cruise census estimate, C_k or C_{kr}, was used to determine the number of eggs produced per day during the spawning season

$$E_d = \frac{C_k}{t_i} \text{ or } \frac{C_{kr}}{t_i} \quad (7)$$

where E_d = daily egg production
t_i is defined under Equation (5).

The seasonal estimate of egg production (E_s) was then determined by plotting the daily egg production against the middate of the cruise representative of the spawning season. The area under the resulting polygon (triangle in this case), determined by planimetry, was then equated with egg production for the entire spawning season. This method assumes a high egg production midseason tapering off to low production at the beginning and end of the spawning season. It approaches a normal distribution of egg production. For species with a short spawning season as in northern anchovy off Oregon and Washington, estimates obtained by this method are about one-half as large as those obtained by the Sette and Ahlstrom Egg Method.

The Saville Egg Method of estimating seasonal egg production (E_s) is based on Saville's (1956, 1964) approach. It assumes that egg production follows a normal distribution throughout the spawning season. A census estimate (C_k or C_{kr}) of eggs obtained from a cruise made during the spawning season represents a proportion of the area under a normal curve. If the duration and peak of the spawning season are known, seasonal egg production (E_s) can be estimated (Houde 1977) as:

$$E_s = \frac{C_k y_i}{x_i t_i} \text{ or } \frac{C_{kr} y_i}{x_i t_i} \quad (8)$$

where y_i = the number of days in cruise i
x_i = the proportion of the area under the normal curve represented by cruise i
t_i is defined under Equation (5).

Duration of the spawning season is assumed to be 62 days, lasting from 15 June to 15 August (see D_i under Equation (5)). The spawning peak is assumed to be the middate, 15 July.

The Smith Larva Method of estimating spawning biomass (B) is modified from the method used

in the CalCOFI program (Smith 1972; Pacific Fishery Management Council footnote 2). It relates the census estimate (C_k or C_{kr}) of northern anchovy larvae to spawning biomass by means of a regression. Smith (1972) demonstrated that in the CalCOFI survey area the annual regional census estimate (sum of four quarterly estimates) of larvae is related to northern anchovy spawner biomass in the following way:

$$B_a = 0.098\, L_a \quad (9)$$

where B_a = anchovy spawner biomass in short tons

L_a = annual regional census estimate of larvae $\times 10^9$ which is the sum of the four quarterly census estimates.

This equation was based on yearly data from 1951 to 1966 and 1969, with the zero intercept forced, giving 18 data points. Data, upon which Smith's (1972) equation was based, can be used to obtain a modification of this relationship, applicable to this study, if certain assumptions are met, or can be accounted for: 1) the same relationship between census estimates of the number of northern anchovy larvae and northern anchovy spawning biomass exists in the northern subpopulation as in the central and southern subpopulations; 2) the larva census estimate obtained from one cruise at the time of peak spawning during the shortened spawning season in the northern subpopulation is equivalent to a quarterly census estimate made during the peak spawning period, i.e., winter or spring quarter (Ahlstrom 1967) in the central subpopulation; 3) conditions, primarily temperature, which influence development time and therefore length of planktonic life, are similar in the northern and central subpopulations for the time periods considered; 4) sampling in the two survey regions is similar; 5) spawning frequency during the time period considered, i.e., during one quarter in the central subpopulation and during the 2-mo spawning season in the northern subpopulation, is the same in both areas.

Data from the Pacific Fishery Management Council (footnote 2) on quarterly larva census estimates for the central subpopulation for winter and spring quarters (Table 1) were regressed on spawner biomass estimates for the years 1951 through 1966 and 1969, 1972, and 1975, with the zero intercept forced, giving 20 data points each.

$$\text{Winter quarter: } B_a = 614 + 0.152\, L_w \quad (10)$$
$$r^2 = 0.70$$

$$\text{Spring quarter: } B_a = 645 + 0.151\, L_s \quad (11)$$
$$r^2 = 0.72$$

where L_w = the winter quarterly regional census estimate of northern anchovy larvae

L_s = the spring quarterly regional census estimate of northern anchovy larvae.

Because Smith's (1972) equation yielded a spawning biomass estimate in short tons, the values obtained in Equations (10) and (11) are also in short tons and may be converted to metric tons (t) by multiplying by 0.9078. Larvae in my study were collected with a 0.333 mm mesh net instead of the 0.55 mm mesh silk net upon which CalCOFI larva census estimates are based (Lenarz 1972; Pacific Fishery Management Council footnote 2). To correct for the increased retention by the smaller mesh net, larva census estimates were divided by the factor given by Lenarz (1972):

$$C_k \text{ corrected} = \frac{C_k}{1.7} \text{ or } C_{kr} \text{ corrected} = \frac{C_{kr}}{1.7}. \quad (12)$$

Thus, in my study I assumed that

$$L_w = L_s = C_k \text{ (or } C_{kr}\text{) corrected.} \quad (13)$$

TABLE 1.—Census estimates (units $\times 10^9$) of *Engraulis mordax* larvae in the central stock for winter and spring quarters and spawner biomass estimates (in 10^3 short tons) of the central stock [from Pacific Fishery Management Council (text footnote 2) A.14 and A.15] from which Equations (10) and (11) were derived (see Methods section).

Year	Winter census	Spring census	Spawner biomass
1951	298	690	180
1952	407	457	156
1953	1,210	373	510
1954	4,469	988	768
1955	5,588	1,709	846
1956	1,911	1,206	485
1957	5,954	4,308	1,172
1958	8,114	5,236	1,479
1959	6,341	8,155	1,514
1960	7,552	7,547	1,540
1961	992	6,714	1,159
1962	4,814	23,567	2,986
1963	17,377	24,818	4,254
1964	8,941	14,383	2,901
1965	19,155	22,690	4,659
1966	15,103	15,865	3,572
1969	19,756	6,538	2,999
1972	8,213	14,335	2,784
1975	29,754	4,071	3,603

Yield Estimates

Because the northern anchovy stock under consideration is in a nearly virgin state, an estimate of potential yield can be obtained using Gulland's (1971) formula

$$Y_{pot} = XMB_0 \quad (14)$$

where Y_{pot} = maximum potential yield
X = a constant coefficient [0.6 for northern anchovy based on MacCall et al. (1976)]
M = instantaneous natural mortality rate [1.00-1.05 for northern anchovy based on MacCall et al. (1976) and Pacific Fishery Management Council (footnote 2)]
B_0 = mean virgin biomass, in this case spawning biomass.

SURVEY RESULTS

Hydrography and Plankton Volume

In all 3 yr, upwelling activity was observed along the coast, evidenced by the colder, <14° C water nearshore (Figures 3-5). This is a typical summer condition when winds blow mainly from the north, currents tend generally to the south, upwelling takes place in a narrow band along the coast with resultant offshore transport of surface waters (Wyatt et al. 1972; Smith 1974; Huyer et al. 1975; Ingraham and Hastings 1976; and others). Offshore, especially beyond the continental shelf, water temperatures were >14° C, well within the range for successful northern anchovy spawning and early development (Brewer 1976).

Salinity contours showed that all three surveys covered the inner bounds of the Columbia River plume, delineated by the 31‰ isohaline (Figures 3-5). The outer bounds of the plume, defined by the 32.5‰ isohaline (Barnes et al. 1972), were not encompassed. This plume is a persistent hydrographic feature off the Oregon coast in summer (Barnes et al. 1972). The Columbia River reaches maximum outflow in June and flows southerly, under the influence of prevailing winds and currents, as a plume of shallow (20-40 m deep), low salinity, warm water on top of the more saline and colder ocean water. It can extend as far as 800 km offshore and as far south as northern California. In 1976 the plume extended farther south and was closer to the coast than in 1975. In 1977 the central core of the plume was much reduced reflecting the extreme drought conditions of that year. High salinities, >33‰, along the coast were indicative of upwelling.

Chlorophyll concentrations at 3 m in 1975 and 1976 were greatest near the coast in regions of upwelling and generally decreased with distance from shore (Figures 3, 4). In 1975, relatively moderate concentrations extended beyond the continental shelf in the region of the lowest salinity plume water. This may be indicative of higher productivity associated with nutrient rich plume waters near the Columbia River mouth (Anderson 1972).

Of the 920 surface drifters released in July 1976, 24 or 2.6% were returned by 21 August 1976 (Figure 6). No additional returns were reported as of February 1977. All but seven of the returns were from the 2 km stations. All returns that had been released off Oregon indicated southward transport. Two returns from the 2 km station near the Columbia River indicated some transport into the river and one return showed northward movement. Three drifters released 46 km off Grays Harbor, Wash., were transported toward the coast while three drifters from the 2 and 9 km stations were transported moderate distances northward. The low number of returns (2.6%) probably reflects the offshore component of surface drift which is generally observed during the summer upwelling season (Wyatt et al. 1972; Huyer 1974).

Plankton volumes, which ranged from 30 to 4,726 ml/1,000 m^3 in 1975 and 8 to 3,670 ml/1,000 m^3 in 1976, were greatest on the continental shelf with the highest volumes (>2,000/1,000 m^3) occurring at stations 2, 9, and 28 km from shore (Figures 3, 4). In these areas the plankton consisted largely of phytoplankton and ctenophores although at 9 and 28 km off Cape Perpetua, Oreg., in 1975 it consisted mainly of copepods and euphausiids. Nearshore low plankton volumes <100 ml/1,000 m^3 were observed at the 2 km stations off Grays Harbor in both 1975 and 1976 and off the Columbia River in 1975. High plankton volumes appeared to be mainly associated with coastal upwelling with no obvious relationship to the Columbia River plume. However, plume waters are a near surface phenomenon while the plankton was sampled from 150 m to the surface possibly obscuring any relationship.

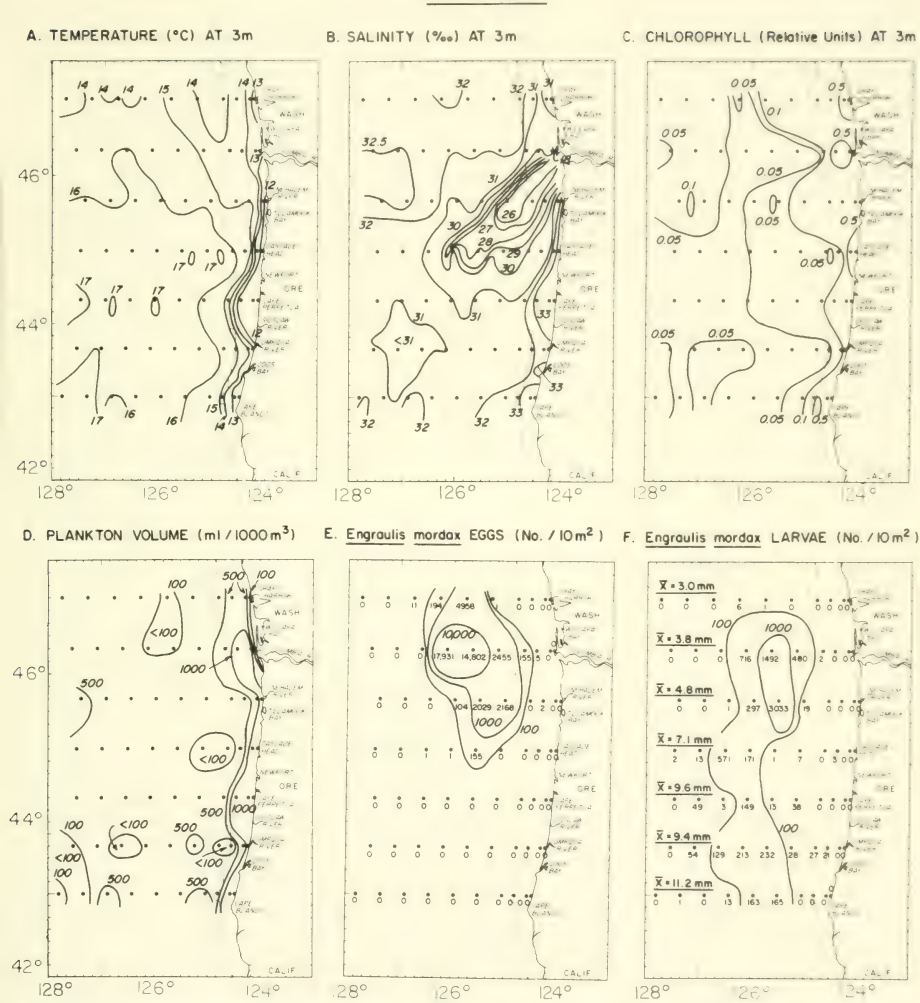


FIGURE 3.—Results from the July 1975 ichthyoplankton survey off Oregon and Washington: hydrography, plankton volume, *Engraulis mordax* eggs and larvae. One chlorophyll unit is equivalent to 46.3 μg coproporphyrin standard 1 or 6.14 μg chlorophyll *a* 1. Mean standard length of northern anchovy larvae on each transect is listed along the left margin of F.

Eggs and Larvae

Northern anchovy eggs were taken at 17 and 23 of the 70 stations sampled in 1975 and 1976 (Figures 3, 4; Table 2). In 1975 the center of egg abundance was north of the Columbia River plume. Largest concentrations, up to 17,931 under 10 m² sea surface, occurred 120-157 km off the mouth of the Columbia River. In 1976, the center of abundance was located 83 km off the Oregon coast

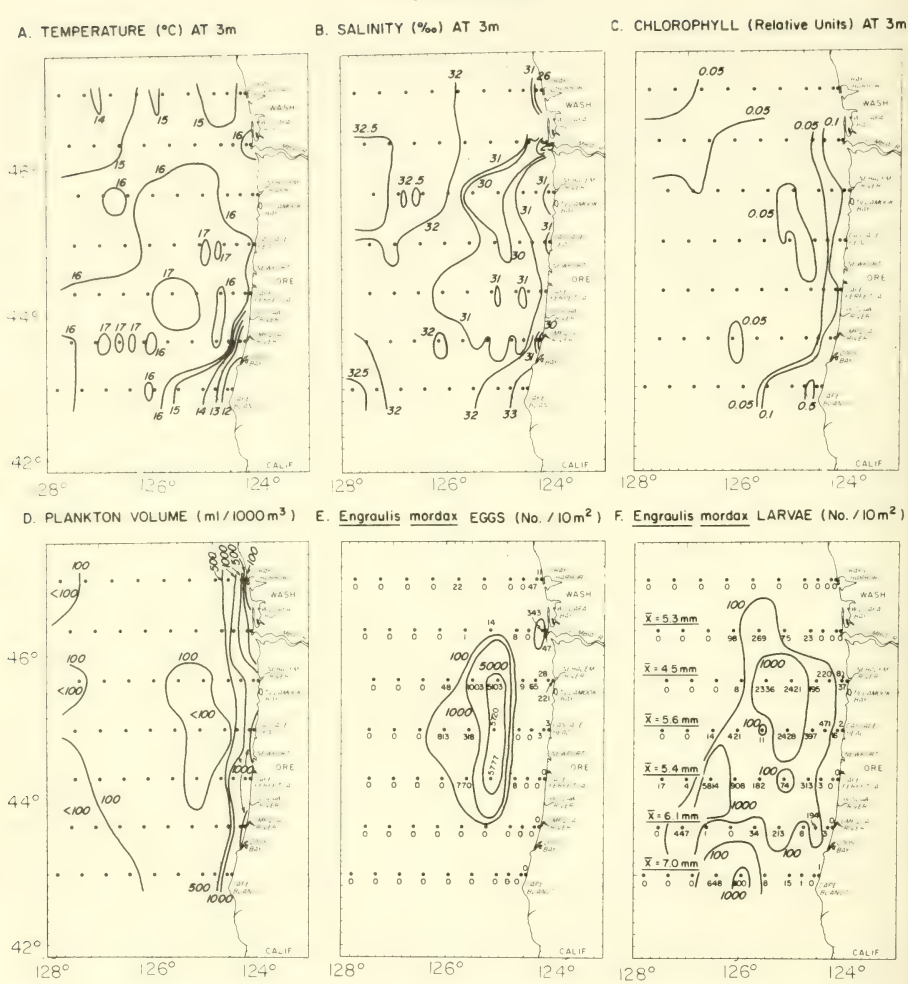


FIGURE 4.—Results from the July 1976 ichthyoplankton survey off Oregon and Washington: hydrography, plankton volume, *Engraulis mordax* eggs and larvae. One chlorophyll unit is equivalent to 46.3 μg coproporphyrin standard/l or 6.14 μg chlorophyll *a*/l. Mean standard length of northern anchovy larvae on each transect is listed along the left margin of F.

between the Nehalem River and Cape Perpetua within the Columbia River plume. The largest egg concentration, 5,777 under 10 m² sea surface, was one-third the highest concentration found in 1975. Overall mean egg abundance was 642 and 291 under 10 m² sea surface in 1975 and 1976, and at positive stations it was 2,645 and 886 under 10 m². In both years the egg distribution was bounded to the south and offshore but not to the north, although relatively few eggs were taken on the

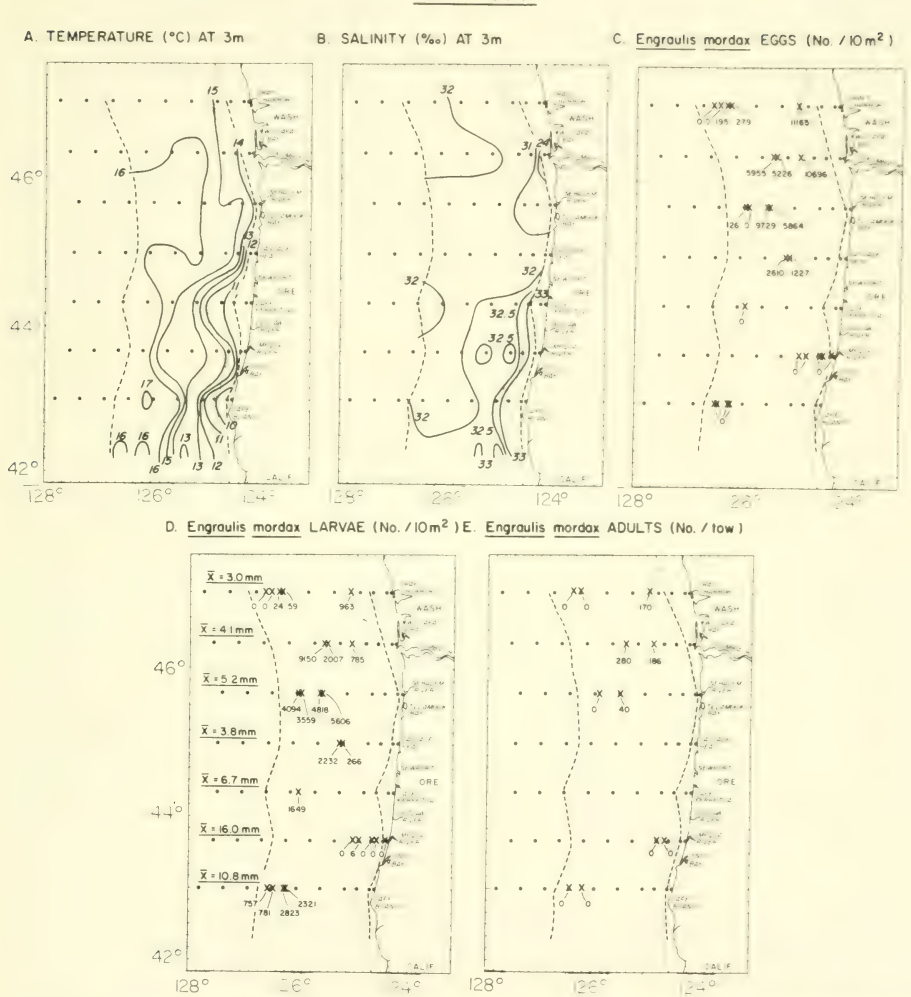


FIGURE 5.—Results from the July 1977 acoustic survey off Oregon and Washington: hydrography, *Engraulis mordax* eggs, larvae, adults. Values for adult catches are based on a 30 min surface tow of a pelagic trawl. Dotted lines delimit east and west cruise track boundary. On C and D, "X" indicates location of the only bongo samples taken during this cruise. On E, "X" indicates location of pelagic trawl stations. Mean standard length of anchovy larvae on each transect is listed along the left margin of D. Data in C and D courtesy of Methot (text footnote 11). Data in E from Smith (text footnote 10).

northernmost transect in 1976. No eggs were taken in regions of active upwelling and few were taken nearshore over the continental shelf except at the 9 km station just north of the Columbia River mouth in 1976 where a patch of warm, <16° C, surface water occurred. The farthest offshore

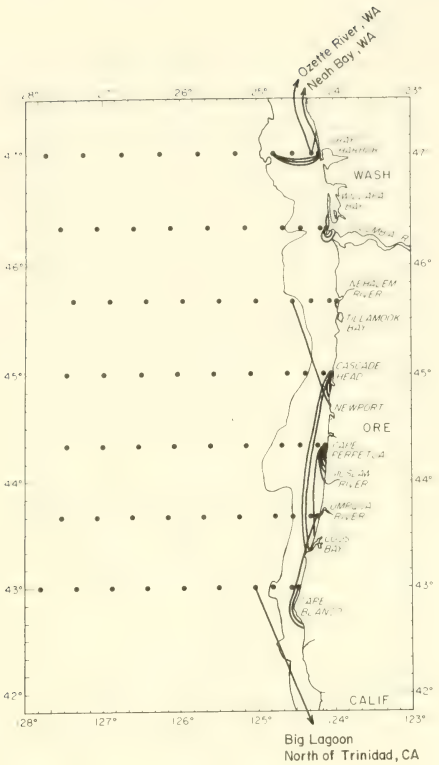


FIGURE 6.—Returns of surface drifters released at the sampling stations off Oregon and Washington during the July 1976 ichthyoplankton survey and returned by 21 August of that year. Lines represent drift paths from release point (sampling station) to return location. Depth contour is 183 m.

TABLE 2.—Summary of collection data on *Engraulis mordax* eggs and larvae off the Oregon-Washington coast from ichthyoplankton surveys conducted in 1975 and 1976. Seventy stations were occupied on each survey.

Item	10-18 July 1975	7-15 July 1976
No. positive stations		
Eggs	17	23
Larvae	33	40
Eggs or larvae	38	45
Eggs and larvae	12	18
Mean no. eggs/10 m²		
All stations	642.49	291.15
Positive stations	2,645.54	886.10
Mean no. larvae/10 m²		
All stations	115.89	278.73
Positive stations	245.82	487.78

that eggs were taken was 194 km and few were found beyond 157 km. All eggs were taken at stations where surface temperatures were >14° C. Mean temperature at 3 m depth at positive stations was 15.18° and 16.09° C and mean salinity was 30.69 and 30.07‰ in 1975 and 1976. Egg concentrations did not correlate with high surface chlorophyll levels and greatest concentrations were in regions of low plankton volumes. Although bongo samples were taken only at trawl stations during the acoustic survey in 1977 (Figure 5) catch trends of eggs were similar to the previous two surveys (Methot[12]). Northern anchovy eggs were taken only on the four northern transects in concentrations up to 11,165 under 10 m² sea surface.

Northern anchovy larvae were more widely dispersed than northern anchovy eggs with 33 and 40 positive stations in 1975 and 1976 (Figures 3, 4; Table 2). Thirty-eight and 45 stations had either eggs or larvae in 1975 and 1976 and 12 and 18 stations had both, respectively. In 1975, highest numbers of larvae, >1,000 under 10 m² sea surface, were found 120 km offshore, near and south of the highest egg concentrations. In 1976, greatest larva concentrations occurred 83 and 120 km offshore between the Nehalem River and Cascade Head, Oreg.; 194 km off Cape Perpetua; and 120 km off Cape Blanco, Oreg. Overall mean abundance was 115 and 278 under 10 m² sea surface in 1975 and 1976, and 487 and 245 under 10 m² at positive stations. In 1975 larvae occurred mainly in a corridor paralleling the coast beyond the continental shelf while in 1976 they were more widely distributed and also occurred closer to the coast. The sampling grid apparently bordered their center of abundance to the north and offshore but not to the south. As with the eggs, larvae were generally not found in regions of active upwelling. Mean length of larvae on each transect in 1975 increased progressively from 3.0 mm in the north to 11.2 mm in the south, evidence of drift south from the spawning center based on egg distributions and seasonal flow patterns. In 1976 mean length of larvae per transect increased from 4.5 mm off the Nehalem River to 7.0 mm off Cape Blanco but the trend was not as pronounced as in July 1975. This reduced trend may be partly a result of decreased northerly winds, evidenced by reduced upwelling, and reduced southward transport compared to 1975.

[12]R. D. Methot, Scripps Institution of Oceanography, Graduate Department, La Jolla, CA 92093, unpubl. data.

Also, based on egg distribution the spawning aggregation appeared more widely distributed in a north-south distance. Mean temperature and salinity at 3 m depth at positive stations in 1975 and 1976 were 15.66° and 15.96° C and 31.07 and 31.28‰, respectively. Distribution of larvae did not correlate with high surface chlorophyll levels and abundance was generally highest in regions of low plankton volume. During the acoustic survey in 1977, northern anchovy larvae were collected (Methot footnote 12) on each transect in concentrations up to 5,606 under 10 m^2 sea surface (Figure 5). No larvae were found in samples taken within 46 km of the coast. Mean length of larvae on each transect again showed an increasing trend toward the south.

Adults

During the acoustic survey in 1977, running ripe adult northern anchovy were collected on the three northern transects (lat. 47°02′ N, long. 124°56′ W; lat. 46°60′ N, long. 126°33′ W; lat. 46°19′ N, long. 124°54′ W; lat. 45°40′ N, long. 125°30′ W) between 56 and 130 km offshore (Figure 5). No adult northern anchovy were collected at trawl stations on the southern two transects. No trawls were made on the transects off Cascade Head or Cape Perpetua.

School concentrations, recorded by sonar, were presented by Smith (footnotes 10, 3). Based on sonar traces and results of the pelagic trawl catches, he concluded schools of spawning adult northern anchovy were centered 83 km offshore in the surveyed area and 37 km south of the Columbia River mouth with the inner edge about 37 km offshore and the western edge between 102 km and 130 km offshore. The northern edge was not defined above lat. 47° N and the southern edge was at lat. 44° N.

EGG AND LARVA CENSUS ESTIMATES

The total area represented by the survey in 1975 and 1976, was 148.81 × 10^9 m^2. Census estimates of the total number of northern anchovy eggs and larvae in that area for each cruise are in Table 3.

TABLE 3.—Egg and larva census estimates (C_k and C_{kr}) and spawning biomass estimates (B) of *Engraulis mordax* in the survey area off Oregon and Washington in 1975 and 1976. Values of parameters used in the biomass estimating procedures are presented except those for K (proportion females) and F (mean fecundity) which are constants, 0.5 and 720. See Methods section for description of procedures and equations.

Spawning biomass estimating method	Year and season	Sette and Ahlstrom Census [1]C_K (units × 10^{11})	Sette and Ahlstrom Census corrected L_W or [2]L_S (units × 10^9)	Days represented by cruise D_i	Days included in cruise Y_i	Proportion of area under normal curve X_i	Time to hatch in days t_i
Sette and Ahlstrom Egg Method [Equations (4) and (5)]	1975	121.98		62			2.73
	1976	54.89		62			2.43
Simpson Egg Method [Equations (4) and (7)]	1975	121.98					2.73
	1976	54.89					2.43
Saville Egg Method [Equations (4) and (8)]	1975	121.98			9	0.3335	2.73
	1976	54.89			9	0.3081	2.43
Smith Larva Method [Equations (10) and (11)]	1975 winter	22.22	1,307				
	1975 spring	22.22	1,307				
	1976 winter	52.06	3,062				
	1976 spring	52.06	3,062				

Spawning biomass estimating method	Year and season	Daily egg production [4]E_d (× 10^{11})	Seasonal egg production E_S (× 10^{11})	Spawning Biomass Estimate [5]B_a (tons)	Spawning Biomass Estimate [6]B (t)	Smith Census [7]C_{Kr} (× 10^{11})	Spawning Biomass Estimate [7]B (t)
Sette and Ahlstrom Egg Method [Equations (4) and (5)]	1975		2,770.24		769,511	95.60	603,094
	1976		1,400.49		389,025	43.32	307,022
Simpson Egg Method [Equations (4) and (7)]	1975	44.68	1,316.27		365,631	95.60	294,933
	1976	22.59	708.87		196,909	43.32	170,694
Saville Egg Method [Equations (4) and (8)]	1975		1,205.82		334,951	95.60	262,506
	1976		659.84		183,289	43.32	144,654
Smith Larva Method [Equations (10) and (11)]	1975 winter			812,664	737,736	17.14	696,479
	1975 spring			842,357	764,692	17.14	723,705
	1976 winter			1,079,424	979,901	41.48	894,074
	1976 spring			1,107,362	1,005,263	41.48	920,001

[1]Equation (2).
[2]Equations (12), (13).
[3]Equation (6).
[4]Equation (7).
[5]Based on Sette and Ahlstrom Census.
[6]Equation (3).
[7]Based on Smith Census.

The Smith Census estimate was always lower than the Sette and Ahlstrom Census estimate. Both estimates were used to calculate spawning biomass of adults.

Larva abundance was not corrected for day-night catch differences. A correction factor could not be derived from the data. No consistent pattern of daytime avoidance was apparent based on cruise plots of night to day catch ratios for each millimeter length class as Houde (1977) demonstrated for clupeid larvae. If daytime avoidance did occur, larva census estimates would be low and in turn biomass estimates would be low. Net avoidance of larvae increases with age and since 94% of the larvae captured in 1975 and 98% in 1976 were ≤10 mm SL (standard length), errors due to avoidance should be small. Also, Smith (1972) made no day-night corrections for the CalCOFI program. Thus data from my study are comparable.

SPAWNING BIOMASS ESTIMATES

These biomass estimates apply only to that portion of the spawning population within the northern subpopulation off Oregon and Washington that was sampled in my survey area. In 1975, the egg concentration (Figure 3) was bounded inshore, offshore, and to the south, but the northern boundary was not encompassed. If major egg concentrations occurred north of the sampling area, the biomass estimates would be low. In 1976, essentially the entire egg concentration was bounded. In both 1975 and 1976, larva concentrations were bounded to the north and offshore, but not to the south. The estimates do not account for any additional spawning concentrations within the northern subpopulation should they exist.

The three methods of estimating spawning biomass based on egg abundance (Sette and Ahlstrom, Simpson, and Saville Egg Methods) include the assumption that northern anchovy spawn only one batch of eggs, those in the most advanced mode and upon which fecundity estimates are based, during the time sampled by the survey. This is particularly critical since the recent work by Hunter and Goldberg (1980) has indicated that a ripe adult northern anchovy can mature a batch of eggs and spawn once every 6 or 7 d in the central subpopulation. In this study the area in which northern anchovy eggs were collected was sampled in 5 d in 1975 and 6 d in 1976. It is assumed that the eggs collected represented no more than a single spawning, because batch 1 would hatch before batch 2 was spawned.

The three egg methods of estimating biomass do not take into account egg mortality. Rates of egg mortality in the ocean are unknown for northern anchovy and could not be determined in this study. Eggs could not be staged due to poor condition resulting from collection techniques. If mortality of spawned eggs were high and disintegration rapid (i.e., dead eggs not occurring in plankton samples), the estimates of total number of eggs spawned would be low and the resulting biomass estimates would also be low. However, Sette and Ahlstrom (1948) obtained similar biomass estimates for *Sardinops caerulea* using two techniques, one that involved aging of eggs and another, the Sette and Ahlstrom Egg Method used in my paper, that did not. Presumably egg mortality was not a major factor influencing their estimates. A similar situation may exist for northern anchovy which also has a relatively short-lived (2 or 3 d) egg stage.

Sette and Ahlstrom Egg Method

The egg census estimate (Table 3) for each cruise was divided by the duration of the egg stage, estimated to be 2.73 d in 1975 and 2.43 d in 1976, Equation (6), to obtain estimates of daily egg production. This value was then expanded to the number of days (62) represented by the cruise, Equation (5). Biomass estimates for each cruise were then obtained, Equation (4).

Estimated spawning biomass using the Sette and Ahlstrom Census was 769,511 t in 1975 and 389,025 t in 1976 (Table 3). Somewhat smaller values were obtained with the Smith Census 603,094 and 307,022 t. Since the method used to derive the Smith Census is merely a simplified version of the method used for the Sette and Ahlstrom Census, biomass estimates based on the latter may be better, at least for the egg data. Confidence limits (95%) based on variance estimates of egg abundance, using methods of Houde (1977), gave a range around the point biomass estimates of ±11-15% for all egg methods. However, the variance estimates were low and statistically not very precise because of the low number of data points and are thus not included here. The Sette and Ahlstrom Egg Method assumes a constant egg production throughout the 62-d spawning season. If egg production tapers off at the

beginning or end of the season, the biomass estimates would be high.

Differences in biomass estimates between the 2 yr based on eggs reflects the fact that more than twice as many eggs were collected in 1975 than in 1976. This could be the result of a decrease in spawning biomass between the years although small sample size is probably just as important. Biomass estimates based on eggs are likely to be more variable than those based on larvae. Northern anchovy is a schooling fish; therefore eggs released from spawning schools are clumped, resulting in a sample of high variance (Pacific Marine Fishery Management Council footnote 2).

Simpson Egg Method

Estimates of daily egg production, Equation (7), 44.68×10^{11} in 1975 and 22.59×10^{11} in 1976 using the Sette and Ahlstrom Census (Table 3) and 35.02×10^{11} and 17.83×10^{11} using the Smith Census, were plotted against the cruise middate. The area under the resulting triangle was then equated with egg production for the entire spawning season, $1{,}316.27 \times 10^{11}$ in 1975 and 708.87×10^{11} in 1976 with the Sette and Ahlstrom Census and $1{,}061.76 \times 10^{11}$ and 614.50×10^{11} with the Smith Census. Biomass estimates were then obtained with Equation (4).

Spawning biomass estimates were 365,631 t in 1975 and 196,909 t in 1976 using the Sette and Ahlstrom Census and slightly smaller with the Smith Census (Table 3). These biomass values are nearly one-half those obtained by the Sette and Ahlstrom Egg Method. This reflects the different assumption of this method regarding egg production where it is high in mid season and low at both ends.

Saville Egg Method

Egg production is assumed to follow a normal curve throughout the 62-d spawning season from 15 June to 15 August. Each cruise within that period represents a proportion of the area under that normal curve. In this study, each cruise was of 9 d duration and was made near the peak of the spawning period. In 1975 the cruise represented 33.35% of the curve and in 1976, 30.81%. Seasonal egg production was then estimated by Equation (8) and biomass by Equation (4).

Estimates of biomass using this method were smaller, 334,951 t in 1975 and 183,289 t in 1976 using the Sette and Ahlstrom Census, than in the two previous methods (Table 3). If egg production is skewed from a normal distribution, large errors could be introduced into the biomass estimate.

Smith Larva Method

This method of estimating spawning biomass assumes that a similar linear relationship exists between numbers of larvae and adult spawning biomass in both the central and northern subpopulations. Although this assumption seems reasonable, the recent fecundity estimate for northern anchovy off California, 340 eggs/g total female weight (Hunter and Goldberg 1980), is considerably less than the fecundity estimate obtained for northern anchovy off Oregon, 720 eggs/g total female weight (Laroche and Richardson 1981). These data indicate it would take more planktonic eggs to represent 1 g of fish in the northern than in the central subpopulation. It follows then that it would also take more pelagic larvae to represent 1 g of fish in the northern subpopulation given that spawning frequency and larval growth and mortality conditions are similar. Thus, biomass estimates obtained by this method may be too high.

Other assumptions of the method seem reasonable (see Methods section). The census estimate obtained from one cruise during the shortened spawning season in the north should be equivalent to a quarterly census estimate obtained during a peak spawning period in the south. Sometimes a quarterly estimate for CalCOFI is based on only one cruise, other times a mean of several cruises. However, my cruise dates were purposefully selected at the time of peak spawning. Sometimes CalCOFI quarterly cruises may be conducted near the beginning or end of a quarter and not necessarily at the peak of spawning. Thus larger numbers of smaller larvae may have been collected in our study, and the relationship between numbers of larvae and biomass may be biased to give a higher biomass estimate in the north.

In general, water temperatures at the time of peak spawning appear to be similar off Oregon and California (Ahlstrom 1959; Baxter 1967) so that growth rates and length of time in the water column are assumed to be similar. Methot (in press) demonstrated that growth rates of larvae in the two subpopulations are similar at similar temperatures.

Sampling techniques used in this study were

similar to those of the CalCOFI program (Kramer et al. 1972) except we used 0.333 mm mesh net on 70 cm bongos vs. 0.55 mm mesh on a CalCOFI net. The difference in mesh sizes can be corrected, Equation (12), but because of the reduced avoidance associated with bongo nets, larva catches may be relatively greater resulting in high census estimates and accordingly high biomass estimates.

Spawning frequency during the 2-mo spawning period in the northern subpopulation is unknown. Hunter and Goldberg (1980) indicated that northern anchovy in the central subpopulation may spawn a batch of eggs every 6 or 7 d during peak spawning. If northern anchovy off Oregon respond differently, additional error would be introduced into the biomass estimate. The higher fecundity of fish in the north may be balanced by less frequent spawning.

Spawning biomass estimates derived from the Smith Larva Method are based on larva abundance. Using the larva census estimates corrected for mesh size differences, Equation (12), biomass estimates were obtained by Equations (10) and (11). These estimates were 737,736 and 764,692 t in 1975 and 979,901 and 1,005,263 t in 1976 with the Sette and Ahlstrom Census and slightly less with the Smith Census, 696,479 and 723,705 in 1975 and 894,074 and 920,001 in 1976. In this case, since the Smith Census is based on procedures and data (Smith 1972) from which Equations (10) and (11) are derived, biomass estimates based upon it are probably better than those based on the Sette and Ahlstrom Census.

Because of diffusion and dispersion and length of the larval period (about 30 d compared with 2-4 d for eggs), larvae are more evenly distributed over a given geographic area than eggs and in turn yield a less variable biomass estimate than eggs (Pacific Fishery Management Council footnote 2). This may, in part, account for the smaller year to year difference in biomass estimates based on larvae compared with those based on eggs. Interestingly biomass estimates based on eggs decreased greatly from 1975 to 1976 while those based on larvae increased.

Most Probable Biomass

Spawning biomass estimates (Table 3) ranged from 262,506 to 769,511 t in 1975 and 144,654 to 1,005,263 t in 1976 (Table 3). The biomass estimate based on acoustic survey of adults in July 1977 was about 800,000 t (Smith footnote 3), using methods given by Smith (1970). A reasonable conclusion is that the actual spawning biomass of northern anchovy in the survey area laid or fluctuated between the extreme values in 1975 and 1976 (Houde 1977) and is probably <1 million t but >100,000 t. This line of reasoning is supported by the fact that the estimates from 1975 and 1976 (for a given method) are within twofold of each other and less than tenfold (for any method) from the acoustic survey.

These estimates only include mature spawning adult fish. Laroche and Richardson (1981) reported that northern anchovy in the northern subpopulation attain first sexual maturity at the end of the second year, i.e., in the third summer. Thus northern anchovy <2 yr old are not included in the estimates and may represent additional sizeable biomass. These immature fish are segregated geographically from spawning adults during the spawning season with the young fish occurring in nearshore coastal areas (Laroche and Richardson 1981).

Based on these estimates, spawning biomass of northern anchovy off the Oregon-Washington coast is less than that in the central subpopulation which had a mean estimate of around 3,631,200 t for 1965-72 (MacCall et al. 1976), although a recent population decline has been recorded in 1978 (1,183,771 t) and 1979 (1,564,139 t) (Stauffer 1980). My spawning biomass estimates are more comparable to that for the southern subpopulation of 544,680 t (mean for 1965-69) (MacCall et al. 1976).

YIELD ESTIMATES

Using Gulland's (1971) formula for potential yield to a fishery, Equation (14), with the range of instantaneous natural mortality rates of 1.0-1.05, estimates for a biomass of 144,654 t are 86,792-91,132 t. For a biomass of 1,005,263 t they are 603,158-633,316 t. These potential yield estimates are about 60% of the spawning biomass, which may be dangerously high values for a species known to undergo large year-to-year fluctuations in abundance.

Recommendations for harvest quotas by the northern anchovy management plan for the central subpopulation called for a more conservative yield estimate of 70% of one-third, or about 23%, of the spawning biomass in excess of 907,800 t (Pacific Fishery Management Council footnote 2).

At an estimated spawning biomass of 3,631,200 t (MacCall et al. 1976) the harvest quota would be 635,400 t or approximately 17% of the total spawning biomass. At the recent reduced biomass level of 1,564,100 in 1979, the optimum yield established for the 1979-80 season in the U.S. Fishery Conservation Zone was 153,100 t (Stauffer 1980), equivalent to only 10% of the total spawning biomass.

Thus the actual realizable yield and in turn the feasibility of establishing a fishery on this northern stock of northern anchovy is difficult to assess. Northern anchovy are considered to be important forage items for fishes such as salmon and albacore off Oregon and Washington but northern anchovy biomass actually consumed by these species has not been adequately estimated. Northern anchovy are also important items in the diet of marine birds. Weins and Scott (1975) estimated that four species of marine birds consume 28,000 t of northern anchovy annually off Oregon.

If the northern anchovy stock off Oregon and Washington could support a harvest of 10% of the total biomass, as in the recent quotas on the reduced biomass for the central subpopulation, a yield of about 14,465-100,526 t might result. If this is reasonable, the feasibility of establishing such a fishery still remains to be determined. Feasibility partly depends on distribution patterns and habits of the stock and on economic considerations, the latter of which is beyond the scope of this paper. Seasonal patterns of distribution were discussed by Laroche and Richardson (1981). The most compact aggregations appear to occur during the spawning season in the offshore spawning center. However, school sizes appear to be small. Smith (footnote 3) estimated that half of the northern anchovy schools counted during the acoustic survey in July 1977 were <4 t and only 1.1% were over 64 t. Small school size could be a deterrent to fishery development.

COMPARISON OF NORTHERN AND CENTRAL SUBPOPULATIONS

Important ecological differences exist between the northern and central subpopulations of *E. mordax* with respect to spawning times and locations and associated environmental parameters. Off California, spawning takes place throughout the year (Figure 7) with a peak occurring between January and April (Smith and Richardson 1977). Off Oregon, spawning takes place over a 2-mo period (Figure 7) with a peak in July, based on the collection of small larvae (Richardson 1973, footnote 5). These differences in peak spawning times certainly contribute to reproductive isolation.

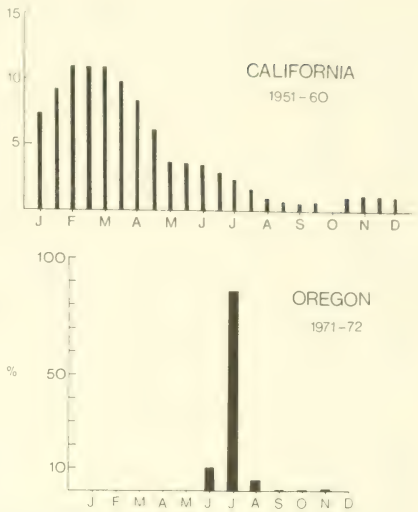


FIGURE 7.—Spawning cycle of *Engraulis mordax* off California and Oregon. Upper graph is after Smith and Richardson (1977). Lower graph is based on catches of northern anchovy larvae given by Richardson (text footnote 5).

Off California (Figure 8), at the initiation of peak spawning southward flow of the California Current is minimal (Saur 1972) with resulting minimal larval transport south away from the spawning area; temperature at 10 m depth (Lasker and Smith 1977) is reaching minimum values in the annual cycle; upwelling is minimal but increasing (Bakun 1973); day length is beginning to increase after the shortest day in December. In contrast, off Oregon (Figure 9), at the time of peak spawning, current flow to the south is at a maximum (Huyer 1977); surface temperatures (Johnson 1961) are reaching maximum values in the yearly cycle (excluding the colder waters of the nearshore upwelling zone); upwelling activity is at a maximum (Bakun 1973); day length is beginning to decrease after the longest day in June.

Off California (Figure 10), spawning takes place closer to the coast (Smith and Duke[13]) than off

[13]Smith, P. E., and S. Duke. 1975. Nearshore distribution of northern anchovy eggs and larvae (*Engraulis mordax*). NOAA NMFS, Southwest Fish. Cent., Admin. Rep. No. LJ-75-58, 15 p.

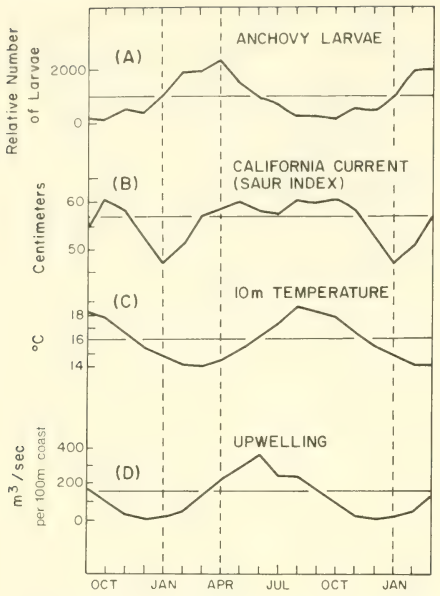


FIGURE 8.—Yearly cycle of *Engraulis mordax* larva abundance and selected environmental parameters [mean annual cycles (1953-60)] off California (reproduced from Lasker and Smith 1976). A) Larva abundance. B) California Current strength indicated by sea level difference approximations (Saur 1972). C) Temperature at 10 m depth. D) Upwelling (Bakun 1973). Dashed lines indicate period of peak spawning between January and April. Horizontal lines are for reference only.

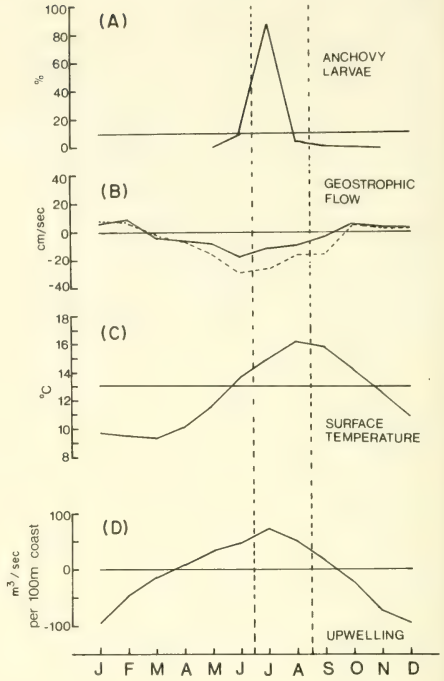


FIGURE 9.—Yearly cycle of *Engraulis mordax* abundance and selected environmental parameters off Oregon. A) Larva abundance in 1971-72 off Newport, Oreg. (Richardson text footnote 5). B) Estimates of alongshore geostrophic flow between 28 and 46 km off Newport at the surface (solid line) and 50 m (dotted line) after Huyer (1977). C) Monthly mean of surface temperatures recorded in six 2° squares off Oregon and Washington (lat. 42°-48° N; long. 124°-128° W) from 1947 to 1958 from Johnson (1961). D) Mean monthly values of upwelling indices for the 20 yr period 1948-67 at lat. 45° N, long. 125° W from Bakun (1973). Dashed lines indicate period of peak spawning. Horizontal lines are for reference only.

Oregon. Relatively little nearshore spawning takes place in the coastal upwelling zone off Oregon which is probably related to the low water temperatures there during the spawning season. Lasker (in press) demonstrated that upwelling may disperse proper-sized food particles, mostly dinoflagellates, and thereby reduce survival of first feeding northern anchovy larvae. These dinoflagellates are replaced by smaller diatoms which are nutritionally inadequate for survival of northern anchovy larvae.

RELATIONSHIP WITH COLUMBIA RIVER PLUME

Data from this study and that by Richardson (1973) provide evidence that a northern anchovy spawning center within the northern subpopulation is closely associated with the Columbia River plume. Reasons for such an association may be related to conditions necessary to induce or trigger spawning in adults or conditions necessary for the survival of the eggs and larvae. Increased river flow and plume size, associated with snow melt and day length, may provide a cue for the offshore spawning migration of adults. Temperature may not be a major factor in the association as both oceanic and plume waters warm to temperatures >13° C (Johnson 1961) needed for spawning, although plume waters warm earlier (Owen 1968).

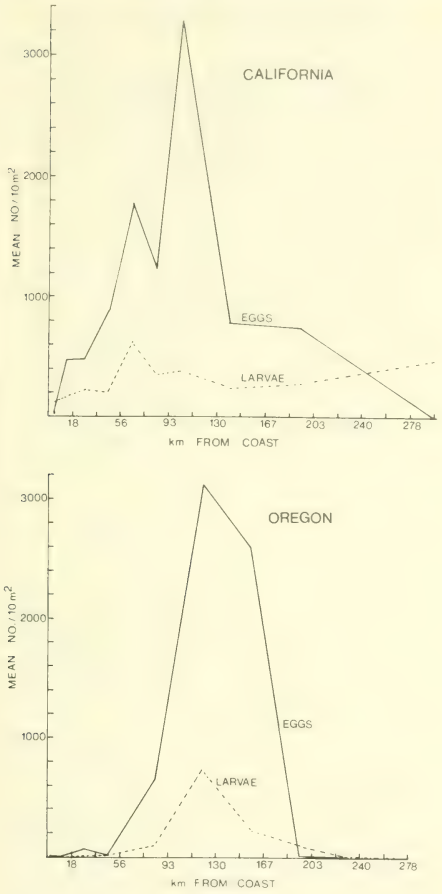


FIGURE 10.—Abundance of *Engraulis mordax* eggs and larvae with distance from the coast off California and Oregon. Upper panel based on data collected off Point Arguello, Calif., in January, April, and July 1964 (Smith and Duke text footnote 13). Lower panel data collected off Oregon and Washington in July 1975.

The plume may provide an optimal environment, in terms of stability and productivity particularly within 100 km or so from the river mouth (Anderson 1972; Barnes et al. 1972), to insure good feeding conditions and enhance survival of first feeding larvae. Such an environment may not exist in the less productive ambient oceanic water or the highly productive but too cold and dynamic coastal upwelling zone. Unfortunately data on type and availability of potential food items in the plume, which would help validate or refute this hypothesis, are not available.

LARVAL TRANSPORT AND JUVENILE NURSERIES

Because of the obvious southward transport of larvae away from the spawning center off Oregon and Washington and the later occurrence of juveniles in Oregon bays and rivers where spawning is apparently rare or unsuccessful, questions arise about return mechanisms. The deep (bottom third of water column) northward flowing countercurrent that develops in late summer beneath southward flowing surface waters (Huyer et al. 1975) could provide a mechanism for reduction of southward transport if larvae utilize it by migrating vertically. Unfortunately we have no depth distribution data on the larvae related to the depth of the shear layer between currents off Oregon to demonstrate this. However, if northern anchovy larvae come to the surface at night to gulp air and conserve energy, as off California (Hunter and Sanchez 1977), then southward and offshore transport would be enhanced, at least at night. Changing wind patterns in the fall from northerly to southwesterly (Wyatt et al. 1972) result in a shift in surface currents from southward to northward, cessation of upwelling, and an onshore drift of surface waters which may contribute to a northerly onshore movement of juveniles. Also, northern anchovy spawned later in the season may not be transported as far south as those spawned earlier and thus would not have to travel as far to return to northern bays and rivers.

An additional offshore spawning center to the north would help explain recruitment of juveniles to the Oregon rivers but there is no evidence for the existence of one, as discussed earlier.

The southward transport of larvae may provide an avenue of gene flow from the northern to central subpopulation.

OTHER SPAWNING CENTERS

Whether the area off the Columbia River is the primary or only spawning center for northern anchovy in the northern subpopulation is unknown. No evidence of spawning to the north exists at least in offshore waters. Also, no evidence is avail-

able for a major spawning center to the south off northern California although that area has not been sampled intensively. It is not known where ripening northern anchovy go after they leave Humboldt Bay in June (Waldvogel 1977), i.e., whether they go north to spawn near the Columbia River plume or whether they spawn off northern California.

Some evidence indicates that another spawning center may occur in the Strait of Georgia. Ripening adults (Pike 1951) and larvae as small as 11 mm (Robinson footnote 6) have been collected there. The environment created by the Fraser River may share similarities with that of the Columbia River plume in terms of stability and productivity (Waldichuk 1957). Thus the region may provide another suitable spawning environment. Additional sampling would be needed for adequate documentation. If a second major spawning center were defined in this region, it would be interesting to investigate the degree of mixing between Columbia River-spawned and Fraser River-spawned northern anchovy.

ACKNOWLEDGMENTS

Special thanks are extended to Paul E. Smith, Southwest Fisheries Center La Jolla Laboratory, NMFS, NOAA, for arranging and conducting an acoustic survey in July 1977 on the NOAA Ship *David Starr Jordan* in cooperation with this research effort and thereby enabling us to obtain a third year of comparative data on hydrography. Thanks are also extended to participants on that cruise, particularly Richard D. Methot, Scripps Institution of Oceanography, who provided data from his collections of anchovy eggs and larvae. I thank George Tinker and his students of Marshfield Senior High School, Coos Bay, Oreg., for making surface drifters and recording returns from the July 1976 cruise. Technical assistance was provided by Barbara Dexter, Joanne L. Laroche, Betsy B. Washington (Oregon State University), and numerous others who helped with the cruises and in sorting samples. Paul E. Smith, Richard D. Methot, and Joanne L. Laroche offered helpful comments on the manuscript.

This work is a result of research sponsored by the Oregon State University Sea Grant College Program, supported by NOAA Office of Sea Grant, U.S. Department of Commerce, under Grant No. 04-6-158-44094.

LITERATURE CITED

AHLSTROM, E. H.
1956. Eggs and larvae of anchovy, jack mackerel, and Pacific mackerel. Calif. Coop. Oceanic Fish. Invest. Prog. Rep. 1 April 1955 to 30 June 1956, p. 33-42.
1959. Vertical distribution of pelagic fish eggs and larvae off California and Baja California. U.S. Fish Wildl. Serv., Fish. Bull. 60:107-146.
1965. Kinds and abundance of fishes in the California Current region based on egg and larval surveys. Calif. Coop. Oceanic Fish. Invest. Rep. 10:31-52.
1966. Distribution and abundance of sardine and anchovy larvae in the California Current Region off California and Baja California, 1951-64: A summary. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 534, 71 p.
1967. Co-occurrences of sardine and anchovy larvae in the California Current region off California and Baja California. Calif. Coop. Oceanic Fish. Invest. Rep. 11:117-135.

ANDERSON, G. C.
1972. Aspects of marine phytoplankton studies near the Columbia River, with special reference to a subsurface chlorophyll maximum. *In* A. T. Pruter and D. L. Alverson (editors), The Columbia River estuary and adjacent ocean waters; bioenvironmental studies, p. 219-240. Univ. Wash. Press, Seattle.

BAKUN, A.
1973. Coastal upwelling indices, west coast of North America, 1946-71. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-671, 103 p.

BARNES, C. A., A. C. DUXBURY, AND B. A. MORSE.
1972. Circulation and selected properties of the Columbia River effluent at sea. *In* A. T. Pruter and D. L. Alverson (editors), The Columbia River estuary and adjacent ocean waters; bioenvironmental studies, p. 41-80. Univ. Wash. Press, Seattle.

BAXTER, J. L.
1967. Summary of biological information on the northern anchovy *Engraulis mordax* Girard. Calif. Coop. Oceanic Fish. Invest. Rep. 11:110-116.

BLACKBURN, J. E.
1973. A survey of the abundance, distribution, and factors affecting distribution of ichthyoplankton in Skagit Bay. M.S. Thesis, Univ. Washington, Seattle, 136 p.

BOLIN, R. L.
1936. Embryonic and early larval stages of the California anchovy *Engraulis mordax* Girard. Calif. Fish Game 22:314-321.

BREWER, G. D.
1976. Thermal tolerance and resistance of the northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 74:433-445.

ELDRIDGE, M. B., AND C. F. BRYAN.
1972. Larval fish survey of Humboldt Bay, California. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-665, 8 p.

GULLAND, J. A.
1971. The fish resources of the ocean. Fishing News (Books) Ltd., Surrey, Engl., 255 p.

HART, J. L.
1973. Pacific fishes of Canada. Fish Res. Board Can., Bull. 180, 740 p.

HOUDE, E. D.
1977. Abundance and potential yield of the round herring,

Etrumeus teres, and aspects of its early life history in the eastern Gulf of Mexico. Fish. Bull., U.S. 75:61-89.

HUBBS, C. L.
1925. Racial and seasonal variation in the Pacific herring, California sardine and California anchovy. Calif. Div. Fish Game, Fish Bull. 8:1-23.

HUNTER, J. R., AND S. R. GOLDBERG.
1980. Spawning incidence and batch fecundity in northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 77:641-652.

HUNTER, J. R., AND C. SANCHEZ.
1977. Diel changes in swim bladder inflation of the larvae of the northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 74:847-855.

HUYER, A.
1974. Observations of the coastal upwelling region off Oregon during 1972. Ph.D. Thesis, Oregon State Univ., Corvallis, 149 p.
1977. Seasonal variation in temperature, salinity, and density over the continental shelf off Oregon. Limnol. Oceanogr. 22:442-453.

HUYER, A., R. D. PILLSBURY, AND R. L. SMITH.
1975. Seasonal variation of the alongshore velocity field over the continental shelf off Oregon. Limnol. Oceanogr. 20:90-95.

INGRAHAM, W. J., JR., AND J. R. HASTINGS.
1976. Seasonal surface currents off the coasts of Vancouver Island and Washington as shown by drift bottle experiments, 1964-65. U.S. Dep. Commer., NOAA Tech Rep. NMFS SSRF-699, 9 p.

JOHNSON, J. H.
1961. Sea surface temperature monthly average and anomaly charts northeastern Pacific Ocean, 1947-58. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 385, 56 p.

KLINGBEIL, R. A.
1978. Sex ratios of the northern anchovy, *Engraulis mordax*, off southern California. Calif. Fish Game 64:200-209.

KRAMER, D., AND E. H. AHLSTROM.
1968. Distributional atlas of fish larvae in the California Current region: northern anchovy, *Engraulis mordax* Girard, 1951 through 1965. Calif. Coop. Oceanic Fish. Invest. Atlas 9, 269 p.

KRAMER, D., M. J. KALIN, E. G. STEVENS, J. R. THRAILKILL, AND J. R. ZWEIFEL.
1972. Collecting and processing data on fish eggs and larvae in the California Current region. U.S. Dep. Commer., NOAA Tech. Rep. NMFS CIRC-370, 38 p.

LAROCHE, J. L., AND S. L. RICHARDSON.
1981. Reproduction of northern anchovy, *Engraulis mordax*, off Oregon and Washington. Fish. Bull., U.S. 78: 603-618.

LAROCHE, W. A.
1976. Larval and juvenile fishes off the Columbia River mouth. Proc. 5th Tech. Conf. Estuaries of the Pacific Northwest, April 1 and 2, 1976. Oreg. State Univ. Eng. Exp. Stn. Circ. 51:17-20.

LASKER, R.
In press. The relation between oceanographic conditions and larval anchovy food in the California Current: Identification of factors contributing to recruitment failure. Proc. Oceanogr. Fish. Symp., Joint Oceanogr. Assem., Edinb., Scotl., Sept. 1976.

LASKER, R., AND P. E. SMITH.
1977. Estimation of the effects of environmental variations on the eggs and larvae of the northern anchovy. Calif. Coop. Oceanic Fish. Invest. Rep. 19:128-137.

LENARZ, W. H.
1972. Mesh retention of larvae of *Sardinops caerulea* and *Engraulis mordax* by plankton nets. Fish. Bull., U.S. 70:839-848.

MACCALL, A. D., G. D. STAUFFER, AND J.-P. TROADEC.
1976. Southern California recreational and commercial marine fisheries. Mar. Fish. Rev. 38(1):1-32.

METHOT, R. D., JR.
In press. Spatial covariation of daily growth rates of larval northern anchovy, *Engraulis mordax*, and northern lampfish, *Stenobrachius leucopsarus*. Rapp. P.-V. Réun. Cons. Int. Explor. Mer.

MCHUGH, J. L.
1951. Meristic variations and populations of northern anchovy (*Engraulis mordax mordax*). Bull. Scripps Inst. Oceanogr. 6:123-160.

MILLER, D. J., AND R. N. LEA.
1972. Guide to the coastal marine fishes of California. Calif. Dep. Fish Game, Fish. Bull. 157, 235 p.

MISITANO, D. A.
1977. Species composition and relative abundance of larval and post-larval fishes in the Columbia River estuary, 1973. Fish. Bull., U.S. 75:218-222.

OWEN, R. W., JR.
1968. Oceanographic conditions in the northeast Pacific Ocean and their relation to the albacore fishery. U.S. Fish Wildl. Serv., Fish. Bull. 66:503-526.

PARSONS, T. R., R. J. LE BRASSEUR, AND W. E. BARRACLOUGH.
1970. Levels of production in the pelagic environment of the Strait of Georgia, British Columbia: A review. J. Fish. Res. Board Can. 27:1251-1264.

PEARCY, W. G., AND S. S. MYERS.
1974. Larval fishes of Yaquina Bay, Oregon: A nursery ground for marine fishes? Fish. Bull., U.S. 72:201-213.

PIKE, G. C.
1951. Age, growth and maturity studies on the Pacific anchovy (*Engraulis mordax*) from the coast of British Columbia. M.A. Thesis, Univ. British Columbia, Vancouver, 44 p.

PRUTER, A. T.
1966. Commercial fisheries of the Columbia River and adjacent ocean waters. Fish. Ind. Res. 3(3):17-68.
1972. Review of commercial fisheries in the Columbia River and in contiguous ocean waters. *In* A. T. Pruter and D. L. Alverson (editors), The Columbia River estuary and adjacent ocean waters; bioenvironmental studies, p. 81-120. Univ. Wash. Press, Seattle.

RICHARDSON, S. L.
1973. Abundance and distribution of larval fishes in waters off Oregon, May-October 1969, with special emphasis on the northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 71:697-711.

RICHARDSON, S. L., AND W. G. PEARCY.
1977. Coastal and oceanic fish larvae in an area of upwelling off Yaquina Bay, Oregon. Fish. Bull., U.S. 75:125-145.

ROACH, S. W., AND J. S. M. HARRISON.
1948. Canning of anchovies. Fish. Res. Board Can., Prog. Rep. Pac. Biol. Stn. 77:108-111.

SAUR, J. F. T.
1972. Monthly sea level differences between the Hawaiian Islands and the California coast. Fish. Bull., U.S. 70:619-636.

SAVILLE, A.
1956. Eggs and larvae of haddock (*Gadus aeglefinus* L.) at Faroe. Scott. Home Dep. Mar. Res. 1956(4), 27 p.
1964. Estimation of the abundance of a fish stock from egg and larval surveys. Rapp. P.-V. Réun. Cons. Perm. Int. Explor. Mer 155:165-170.

SETTE, O. E., AND E. H. AHLSTROM.
1948. Estimations of abundance of the eggs of the Pacific pilchard (*Sardinops caerulea*) off southern California during 1940 and 1941. J. Mar. Res. 7:511-542.

SIMPSON, A. C.
1959. The spawning of the plaice (*Pleuronectes platessa*) in the North Sea. Fish. Invest. Minist. Agric. Fish. Food (G.B.), Ser. II, 22(7), 111 p.

SMITH, P. E.
1970. The horizontal dimensions and abundance of fish schools in the upper mixed layer as measured by sonar. *In* G. B. Farquhar (editor), Proceedings of the International Symposium on Biological Sound Scattering in the Ocean, p. 563-600. MC Rep 005. Maury Cent. Ocean Sci., Dep. Navy, Wash., D.C.
1972. The increase in spawning biomass of northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 70:849-874.

SMITH, P. E., AND R. LASKER.
In press. Position of larval fish in an ecosystem. Proc. IABO Oceanogr. Symp., "Dynamics of Ecosystems," Joint Oceanogr. Assem., Edinb., Scotl., Sept. 1976.

SMITH, P. E., AND S. L. RICHARDSON (editors).
1977. Standard techniques for pelagic fish egg and larva surveys. FAO Fish. Tech. Pap. 175, 100 p.

SMITH, R. L.
1974. A description of current, wind, and sea level variations during coastal upwelling off the Oregon coast, July-August 1972. J. Geophys. Res. 79:435-443.

STAUFFER, G. D.
1980. Estimate of the spawning biomass of the northern anchovy central subpopulation for the 1979-80 fishing season. Calif. Coop. Oceanic Fish. Invest. Rep. 21: 17-22.

WALDICHUK, M.
1957. Physical oceanography of the Strait of Georgia, British Columbia. J. Fish. Res. Board Can. 14:321-486.

WALDVOGEL, J. B.
1977. Age, maturity and distribution of northern anchovy, *Engraulis mordax*, in Humboldt Bay, California. M.S. Thesis, Humboldt State Univ., Arcata, Calif., 36 p.

WIENS, J. A., AND J. M. SCOTT.
1975. Model estimation of energy flow in Oregon coastal seabird populations. Condor 77:439-452.

WILLIAMSON, H. C.
1929. The pilchard and its associates. Mus. Art Notes 4:105-108. [In Pike (1951), not seen by author.]

WYATT, B., W. V. BURT, AND J. B. PATTULLO.
1972. Surface currents off Oregon as determined from drift bottle returns. J. Phys. Oceanogr. 2:286-293.

ZWEIFEL, J. R., AND R. LASKER.
1976. Prehatch and posthatch growth of fishes—a general model. Fish. Bull., U.S. 74:609-621.

VOLUNTARY SWIMMING SPEEDS AND RESPIRATION RATES OF A FILTER-FEEDING PLANKTIVORE, THE ATLANTIC MENHADEN, *BREVOORTIA TYRANNUS* (PISCES: CLUPEIDAE)

ANN G. DURBIN,[1] EDWARD G. DURBIN,[1] PETER G. VERITY,[1] AND THOMAS J. SMAYDA[2]

ABSTRACT

Voluntary swimming speeds and respiration rates of a group of adult Atlantic menhaden (mean wet weight = 302 g) were measured before, during, and after a 7-hour feeding period, during which the diatom *Ditylum brightwelli* was made available at a constant rate. Total ration for the 12 fish ranged between 9.60 and 94.79 g dry weight. Temperature was 20°±1° C. In the absence of food, the routine swimming speeds and respiration rates of the menhaden were: mean ± 95% confidence limits = 12.2±1.6 cm per second (0.47±0.06 body lengths per second), and 0.10±0.009 mg O_2 per gram per hour. During feeding the fish increased their voluntary swimming speed 2.4- to 3.5-fold, and their respiration rates 2.2- to 5.4-fold above the routine rates, depending on the concentration of plankton in the water. There was a linear relationship between $\log_{10}$ respiration rate and mean swimming speed during the feeding and the postfeeding periods. During feeding, the metabolic cost per increment in swimming speed was about 2.5 times higher than the cost of swimming in other species; this is believed to reflect a high energetic cost of filter feeding. There was an approximately hyperbolic relationship between the voluntary swimming speed of the Atlantic menhaden, and the phytoplankton chlorophyll *a* concentration in the water. The swimming speed and respiration rate of the fish remained constant as long as the input of phytoplankton into the tank continued at a constant rate. After feeding, the activity levels and respiration rates of the menhaden quickly returned to prefeeding routine rates.

The Atlantic menhaden, *Brevoortia tyrannus*, is a schooling, filter-feeding planktivore (Peck 1894; Durbin and Durbin 1975) which supports a major commercial fishery along the Atlantic coast of the United States.

The present study investigates voluntary swimming speeds and oxygen consumption rates of Atlantic menhaden before, during, and after a 7-h period during which the fish were fed a ration of the diatom *Ditylum brightwelli*. During this period the plankton was made available at a constant rate, so that feeding was continuous and the ingestion rate was constant. The prolonged feeding was designed to reproduce, as much as possible, natural feeding conditions for menhaden. During these experiments ammonia and dissolved organic nitrogen excretion rates, feces production rates, and assimilation efficiencies were also measured and will be reported in a second paper. These studies are part of a larger effort to determine the energy budget of Atlantic menhaden in Narragansett Bay, R.I.

METHODS

Adult Atlantic menhaden were dipnetted from a commercial purse seine, 2-3 min after it had been set around a school. These fish were transferred to a round, 1.2 m diameter tank and brought in good condition to the laboratory. There the fish were maintained outdoors, in a circular fiber glass tank 1.85 m in diameter and 0.76 m deep, supplied with flowing unfiltered seawater. The tank was protected by a large fiber glass canopy.

Five days after capture, the number of fish in the tank was reduced to 25. Once a day the fish were fed a ration of Rangen's[3] salmon feed, size 00 powder, equivalent to 3% of their dry body weight per day. Within 3 wk all fish fed readily in the tank. The fish were held for 6 wk before use in experiments. During this period, the tank was cleaned every day, and preliminary trials were carried out. This enabled the fish to become accustomed to routine sampling procedures, to the presence of observers near the tank, and also to the presence of a clear Plexiglas cover, which was lowered onto the surface of the tank water during respiration mea-

[1]Graduate School of Oceanography, University of Rhode Island, Kingston, RI 02881.
[2]Department of Oceanography, University of Washington, Seattle WA 98195.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Manuscript accepted March 1980.
FISHERY BULLETIN: VOL. 78, NO. 4, 1981.

surements. The experiments were conducted in the same tank in which the fish were maintained. This removed two potential problems: first, the possibility of injury to the fish as a result of frequent handling; and second, the possibility of stress resulting from recent handling and transfer of the fish to an unfamiliar tank. Stress has been shown to affect the respiration rate and swimming performance of schooling fishes (i.e., Skazhina 1975; Hartwell and Otto 1978).

One week before the experiments were begun, one-half of the fish were removed for length and weight determination, leaving 12 Atlantic menhaden in the tank. We have found that 12-15 adult fish is an optimum number for a tank of this size; fewer fish begin to show signs of stress, whereas more fish begin to interfere with each other during feeding. Experiments were carried out between 26 July and 9 September 1977. At the end of this period the fish were sacrificed for length and weight determination. All fish appeared to be in excellent condition thoughout the experimental period, and showed no evidence of injury or disease.

Experimental Procedure

The experiments were carried out at 20°±1.0° C and a salinity of 31‰. Prior to each experiment, the bottom and walls of the tank were thoroughly cleaned with a wire brush. The fish were fed their normal ration, and then deprived of food for 36 h until the beginning of the experiment to permit evacuation of the intestine and to avoid any effect of the previous meal on the metabolism of the fish. During this 36-h period, the seawater inflow was filtered through a GAF polypropylene bag filter of 5 μm nominal pore size. Feces from the last meal were periodically siphoned from the tank. On the evening before the experiment, the tank walls were again scrubbed and the tank rapidly flushed several times with filtered seawater.

Each experiment was begun at approximately 0630 h, with an initial baseline measurement of respiration rate and voluntary swimming speed of the unfed fish. Plankton was then added to the tank at a constant rate during a 7-h period from approximately 0800 to 1500 h. During each experiment, respiration rates and voluntary swimming speeds were measured on 10 occasions, termed "measurements," which lasted for about 1 h when the fish were feeding, and 1½-2 h when they were not. These measurements correspond to the following periods: no. 1, initial (unfed for 36 h); no. 2-4, feeding during the 7-h period of food input; no. 5, the transition from feeding to postfeeding; no. 6-8, during the first 10 h following feeding; and no. 9 and 10, the next morning, 15-20 h after feeding.

To prevent an excessive accumulation of ammonia in the tank when the fish were fed the larger rations, the tank was flushed briefly with filtered water at the conclusion of feeding.

Food

The solitary diatom *Ditylum brightwelli* was used as food in the experiments. These large cells (~80 μm long) are readily eaten by menhaden. Phytoplankton was raised in outdoor batch cultures. Narragansett Bay water was filtered into 400 l fiber glass tanks, using a series of four cartridge filters culminating in a Gelman 0.45 μm membrane filter, and then enriched to the level of Guillard's F/2 (Guillard and Ryther 1962).

Large volumes (up to 2,500 l) of culture were raised for each experiment, and it was necessary to concentrate the cells before feeding them to the fish. Since the duration of the feeding period was 7 h, the culture was divided into seven batches of equal volume. Each batch was concentrated by gentle back filtration into a volume of 18 l, which was then subsampled by filtering onto a precombusted glass fiber filter for determination of the C and N concentration (Hewlett Packard Model 185B CHN Analyzer). On several occasions additional subsamples were centrifuged to form a pellet, from which the water was aspirated off, and the C, N, ash (combustion at 475° C for 4 h), caloric (Parr adiabatic bomb calorimeter), and Si (Durbin 1977) contents were determined. Each 18 l batch of food was slowly siphoned into the tank over a 1-h period, to provide an approximately constant rate of input of food. By changing the concentration of plankton in these batches, different concentrations of food in the tank and different ration sizes could be obtained. The volume of water added with the food was balanced by the volume removed during sampling, and thus the volume in the tank (1,400 l) remained approximately constant. The chlorophyll *a* concentration in the tank was also periodically determined by fluorometry (Yentsch and Menzel 1963; Lorenzen 1966).

Turbulence produced by the fish stirred the tank and kept the plankton in suspension. The Atlantic menhaden were estimated to filter 13-20% of the tank volume per minute, removing the *D.*

brightwelli with an efficiency of about 25% (Durbin and Durbin 1975).

Respiration Rate

Oxygen consumption by the fish was determined by closed system respirometry. The water in the tank was sealed from contact with the atmosphere by means of a circular cover made of clear 1.2 cm Plexiglas, suspended on pulleys over the tank, which could be gently lowered onto the water surface. Replicate water samples for oxygen determinations (Strickland and Parsons 1972) were siphoned from the tank through a sampling port every 12 min during feeding measurements, and every 20 min during nonfeeding measurements. The precision of the method was ± 0.019 mg O_2/l. Measurements of oxygen from different locations in the tank demonstrated that the movement of the fish kept it well mixed at all times. Control measurements on the tank, filtered seawater, and tank water after the addition of phytoplankton demonstrated that these did not contribute significantly to the change in oxygen content of the water during respiration measurements. The oxygen level in the tank was not allowed to drop by more than 2 mg/l during any measurement; between measurements, the lid was raised off the surface of the water, and air was bubbled through the airstones along the tank walls. The decline of oxygen in the tank with time was linear, with a correlation coefficient of 0.98 or better in all cases; the mean respiration rate of the fish was calculated from the slope of this regression. Ninety-five percent confidence limits (CL) were computed for the slope and used to calculate the 95% CL for the respiraton rate in each measurement. Respiration rates are reported as milligrams oxygen consumption per gram wet weight of fish per hour (mg O_2/g per h).

Swimming Speed

During the respiration measurements the swimming behavior of the fish was recorded with a Sankyo ES-44XL 8 mm movie camera, equipped with a wide angle lens and a remote control and mounted above the tank. The fish were photographed with Kodak Ektachrome 160 film, exposed at 9 frames/s. Paired 10 s shots, 1 min apart, were taken every 6-10 min while the fish were feeding, and every 15-20 min when they were not feeding. Films were later analyzed using a Kodak Model MPG-TH microfilm reader at a magnification of 34×. A sheet of clear acetate was placed over the viewing screen, and the location of each fish was plotted at every fifth frame (the corresponding time interval at 9 frames/s = 5/9 s) when the fish were feeding and swimming rapidly, and every 10th frame (or, every 10/9 s) when the fish were not feeding and swimming slowly. These measurements were then converted to swimming speed in centimeters per second and body lengths (BL) per second. Vertical travel by the fish, which was not corrected for in this method, was negligible since the fish tended to maintain themselves at middepth in the water column.

During each measurement of oxygen consumption, an average of 680 observations of swimming speed were obtained. The average swimming speed during each measurement was determined from the mean of all observations ±95% CL. The distribution of swimming speeds within each measurement was compared with a normal curve. Measurements were compared by first testing for homogeneity of variance, and when appropriate the significance of the difference between means was tested using analysis of variance. When variances were nonhomogeneous, differences between means were tested according to a nonparametric test.

The mean values of each measurement were used to determine the relationship between swimming speed and respiration rate. Measurements were grouped into three categories: initial and final (unfed), feeding, and postfeeding. In the latter two categories there was a linear relationship between swimming speed and log oxygen consumption. Predictive regressions of Y on X are presented to permit the comparison of present results with those in earlier studies. However, we also present the functional regressions (GM) (Ricker 1973), which represent the geometric mean of the regression of Y on X and the reciprocal of the regression of X on Y. Although there has been some controversy on the subject (Jolicoeur 1975; Ricker 1975) the functional regression nevertheless appears to be the preferable method of describing the data. Differences in the slopes and elevations of the regressions were tested for significance by covariance analysis.

RESULTS

The menhaden were 3 yr old, with a mean fork length of 25.8 cm (range 23.0-27.9 cm), a mean wet

TABLE 1.—Basic data on feeding experiments with a school of 12 Atlantic menhaden, total wet weight = 3,624 g. Oxycalorific coefficient used was 4.7 cal/ml of oxygen consumed (Kleiber 1961). Column numbers, in brackets, are for text reference.

Experiment no. (1)	Total ration		Total respiration in excess of routine during the 7-h feeding period			Total respiration in excess of routine during the postfeeding period		
	G dry wt (2)	Kcal (3)	MgO_2 (4)	Kcal (5)	% of ration kcal (6)	MgO_2 (7)	Kcal (8)	% of ration kcal (9)
6	94.79	177.4	10,220	33.62	19.0	1,812	5.96	3.36
4	86.93	162.7	10,075	33.15	20.4	2,040	6.71	4.13
5	67.46	126.3	9,640	31.72	25.1	1,634	5.38	4.26
9	27.64	51.7	5,871	19.32	37.4	286	0.94	1.82
7	20.76	38.9	4,711	15.50	39.8	315	1.04	2.66
8	15.43	28.9	3,914	12.88	44.6	496	1.63	5.65
10	9.60	18.0	2,979	9.80	54.4	573	1.89	10.47

weight of 302 g (range 248-346 g), and a mean dry weight of 104 g.

The food rations ranged from 0.79 to 7.8% of the dry weight of the fish, and thus during the 7-h feeding period the fish fed at rates equivalent to 0.11-1.11% of their dry weight per hour (Table 1).

In a filter feeder such as the Atlantic menhaden, the food ration obtained depends on the volume of water filtered, corrected for the filtration efficiency of the gill rakers. The volume filtered is essentially cylindrical, with cross-sectional area equal to the area of the fish's open mouth, and length equal to the distance swum by the fish in a unit of time. It is shown below that the fish swam at about the same average speed during feeding, and since all fish were of similar size, each fish filtered an approximately equal volume of water during the 7-h feeding period. Thus we assume that each fish obtained the same proportion (1/12) of the plankton added to the tank.

The behavior of the fish followed the same general pattern in all experiments (Figures 1, 2). The voluntary swimming speeds and respiration rates of the fish were low during the initial measurement and then abruptly increased severalfold over the initial rates during feeding. When the input of food was stopped, the fish rapidly filtered the remaining plankton from the water, decreasing their swimming speed and respiration rate as the plankton levels dropped. During the postfeeding period there was a gradual return to prefeeding activity levels and respiration rates, a transition which was completed before the final two measurements on the following morning.

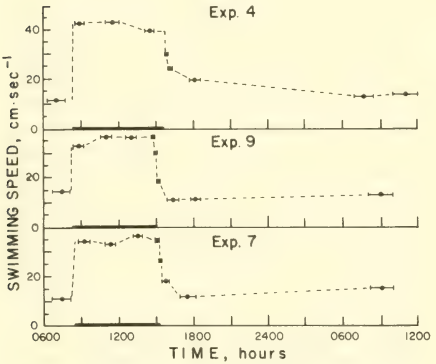


FIGURE 1.—Mean voluntary swimming speed of a school of 12 Atlantic menhaden before, during, and after a 7-h period (indicated by the heavy line on the x-axis) during which they were fed, at a constant rate, a ration of the diatom *Ditylum brightwelli*. Three representative experiments are shown, in which total rations were: no. 4, 162.7 kcal; no. 9, 51.7 kcal; no. 7, 38.9 kcal. The 95% confidence limits were enclosed by the symbols; horizontal bars indicate the duration of each experiment.

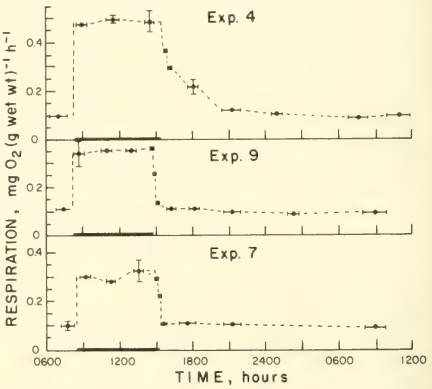


FIGURE 2.—Mean respiration rate for Atlantic menhaden in the measurements presented in Figure 1. The 95% confidence limits are shown by vertical bars when they exceed the size of the symbol.

In most measurements the distribution of swimming speed observations showed small but statistically significant ($\chi^2 < 0.01$) departures from normality. These usually took the form of a slight positive skewness, and leptokurtosis (data values concentrated in the region of the mean).

The variance of the swimming speed, which included the variability shown by each individual fish, as well as differences among fish, was positively correlated with the mean. However, the coefficient of variation revealed that the fish were relatively more variable in their swimming behavior when they were not feeding (Figure 3). These results confirmed qualitative observations during the experiments that the fish were least excitable, and most consistent in their swimming behavior, when they were engaged in feeding.

With the exception of measurement no. 5, which bracketed the transition from feeding to postfeeding, the fish were very consistent in their swimming behavior and respiration rate during individual measurements. Thus the 95% CL about the estimates of mean respiration rate and swimming speed during each of the measurements were small, averaging ±8.9% of the mean respiration rate and ±2.3% of the mean swimming speed.

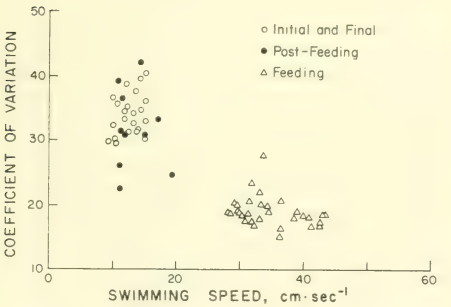


FIGURE 3.—Relationship between mean and coefficient of variation ($\sigma/\bar{x}$ [100%]) in the swimming speeds of a school of 12 Atlantic menhaden during the initial and final, feeding, and postfeeding measurements.

Initial and Final Measurements (No. 1, 9, 10)

These may be termed "routine" (Fry 1957) since the fish were unfed and spontaneously active. During these measurements the fish swam slowly about the tank without showing any strong schooling patterns. The mean swimming speeds and respiration rates were very similar during the initial and final measurements (Table 2). The range among the mean voluntary swimming speeds of the measurements was also fairly small, 10.5-15.2 cm/s (0.41-0.59 BL/s) (Figure 4). The range among

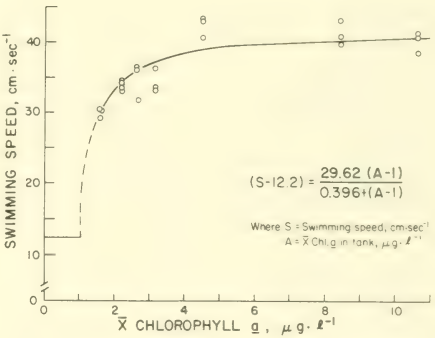


FIGURE 4.—Hyperbolic relationship between voluntary swimming speed (S) of a school of 12 Atlantic menhaden feeding on *Ditylum brightwelli*, and chlorophyll *a* concentration in the water (A). The three measurements of mean swimming speed obtained during the 7-h feeding period of each experiment are plotted as a function of the mean chlorophyll *a* concentration during each experimental feeding period.

TABLE 2.—Swimming speeds (S) and respiration rates (R) of Atlantic menhaden in the feeding experiments and their regression equations.

Measurements (periods)	Mean ± 95% confidence limits: Swimming speed cm/s	Respiration rate mg O_2/g per h
Initial (no. 1)	12.2±1.6	0.10 ±0.009
Final (no. 9, 10)	13.4±1.2	0.093±0.007

	Derived regressions: Predictive	Functional (GM)
Feeding (no. 2, 3, 4)	$\log_{10}R = 0.0271\,(S) - 1.446$ Equation (2); $r = 0.918$, SE slope = 0.0026	$\log_{10}R = 0.0295\,(S) - 1.534$ Equation (3)
Postfeeding (no. 6, 7)	$\log_{10}R = 0.0293\,(S) - 1.276$ Equation (4); $r = 0.856$, SE slope = 0.0062	$\log_{10}R = 0.0342\,(S) - 1.342$ Equation (5)

the respiration rates was similarly narrow and did not show any clear relationship with swimming speed (Figure 4).

Feeding Measurements (No. 2, 3, 4)

As soon as food was added, the fish began "tasting" the water by flaring their opercula and swimming rapidly forward for a few seconds. After 1-2 min they began to feed, circuiting the tank and swimming in the same direction at about the same speed. Within each experiment, the mean voluntary swimming speed and the associated respiration rate remained nearly constant throughout the entire 7-h feeding period (Figures 1, 2). The mean swimming speed was established during the first 15 min of feeding and was related to the amount of plankton in the water (Figure 4). Within a range of about 1.5-4 μg chlorophyll *a*/l the voluntary swimming speed and respiration rate of the fish were roughly proportional to the chlorophyll *a* content of the water. Above about 4 μg chlorophyll *a*/l however, the swimming speed was independent of plankton concentration. In the three high-ration experiments during feeding, the mean speed $\pm 95\%$ was 41.3 ± 1.5 cm/s and the corresponding mean respiration rate was 0.48 ± 0.029 mg O_2/g per h. The relationship between chlorophyll *a* concentration and the voluntary swimming speed can be described by a rectangular hyperbola [Equation (1), see Figure 4]. The zero point for the curve was taken as the mean swimming speed of unfed fish (12.2 cm/s) and the approximate concentration threshold (1 μg chlorophyll *a*/l) (Durbin and Durbin 1975) of *D. brightwelli* at which Atlantic menhaden will begin to feed.

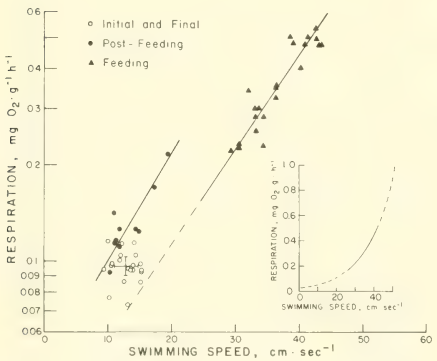


FIGURE 5.—Relationships between mean voluntary swimming speed and mean respiration rate of a school of 12 Atlantic menhaden. The $\bar{x}$ and 95% confidence limits of the initial and final measurements are shown; functional regressions shown for the feeding and postfeeding measurements are presented in Table 2. Inset is an arithmetic plot of Equation (3); extrapolations beyond observed data are dashed.

In these experiments the mean voluntary swimming speed of the Atlantic menhaden during feeding ranged between 29.3 and 43.4 cm/s (1.14-1.68 BL/s). This represented a 2.2-3.3 fold increase over the mean prefeeding routine swimming speed (12.2 cm/s). Respiration rates during feeding ranged between 0.221 and 0.538 mg O_2/g per h and were thus elevated 2.2-5.4 fold over the mean initial routine respiration rate (0.10 mg O_2/g per h). There was a good linear relationship between the mean swimming speed during feeding and the $\log_{10}$ transformed mean respiration rate (Figure 5, Table 2).

Postfeeding Measurements (No. 6, 7, 8)

When the input of food was stopped at the end of 7 h, the fish rapidly depleted the plankton remaining in the tank. Within 5 min the swimming speed of the fish decreased noticeably, and as plankton levels continued to decline, the fish progressively reduced their swimming speed (Figure 1, measurement 5). Respiration rates also declined (Figure 2). Feeding usually became intermittent within 15-20 min, and ceased entirely during the next one-half hour, at which time the plankton in the tank had been reduced to a negligible level.

After the Atlantic menhaden had removed the last of the plankton, they continued to "taste" the water fairly frequently and were somewhat restless, as though searching for additional food. During this postfeeding period, however, there was a gradual return toward the prefeeding behavior. Dusk arrived during or shortly after the second postfeeding measurement. Although it was not possible to photograph the fish during the third postfeeding measurement at midnight, their activity levels appeared to be very low as indicated by their low respiration rates, and qualitative observations of their swimming behavior in the dim light.

The postfeeding measurements were spaced too far apart to precisely define the time by which the fish returned to their routine activity and metabolic levels. In general the duration of this

period was greater with larger ration sizes (~4.5 h, experiment 4); at low food levels (e.g., experiments 7, 9) the respiration rate had essentially returned to baseline in <2 h (Figure 2).

The mean swimming speed of the first two postfeeding measurements (no. 6, 7) usually fell within the range of the routine swimming speeds; however, the respiration rates tended to be elevated above the routine rates (Figure 5). There was a linear relationship between mean swimming speed and $\log_{10}$ respiration rate in these postfeeding measurements (Figure 5, Table 2).

DISCUSSION

These results demonstrate that the voluntary swimming speed of adult Atlantic menhaden is related to the availability of plankton food in the water. If food is not present, the voluntary swimming speed and respiratory rate of Atlantic menhaden are low. Swimming speed increases during feeding, following an approximately hyperbolic relationship with increasing plankton density in the water. Over a wide range of plankton concentrations the characteristic swimming speed of the menhaden is about 1.60 BL/s, with a respiratory rate of about 0.48 mg O_2/g per h. This approximately 5-fold increase in respiratory rate above the routine implies that the energy expenditures during feeding will be a major element in the energy budget of menhaden.

Previous descriptions of menhaden feeding behavior (Durbin and Durbin 1975), based on short-term experiments in which the plankton concentration decreased during the course of each experiment, were generally confirmed by the present study. However, respiration rates measured in the present study indicate that the feeding frenzy, which was observed in the earlier study after a large amount of zooplankton was added to the tank, is not likely to persist during prolonged feeding in nature. Swimming speeds during the frenzy were estimated to be about 2-2.5 BL/s. The energy cost of swimming at these speeds, as estimated from Equation 3 (Table 2), would be high (10-23 times the routine metabolic rate) and would not appear to be bioenergetically profitable over prolonged periods.

The same general behavior patterns have been observed in five groups of Atlantic menhaden collected during three summers. Such consistency indicates that the behavior of the Atlantic menhaden in the laboratory can provide insight into their behavior in the field. However, these laboratory based predictions of menhaden swimming speeds need to be tested in the field.

Satiation has often been observed to be an important feature which affects the feeding behavior of fishes (i.e., Ivlev 1961). This is most evident for "macrophageous" fishes (those which take their food in large particles). In the present study, however, there was no evidence of satiation even with the largest ration, when the fish consumed the equivalent of 8% of their body weight during a 7-h period. Evidence of satiation would include a decrease in their swimming speed during the experiments or a switch to intermittent feeding. In contrast, the fish fed continuously at a constant rate as long as food was available, and they continued to search for food after it stopped coming into the tank. Plankton densities sufficient to saturate the physical capacity of menhaden to handle and process food may not be of much ecological significance. This is because natural plankton populations in the size range which can be filtered by menhaden are seldom found in concentrations greater than those used in the present experiments. The high concentrations of chlorophyll *a* which occur in coastal and estuarine waters during the summer are primarily small flagellates (e.g., Durbin et al. 1975), which are too small to be retained on the gill rakers of the menhaden (Durbin and Durbin 1975).

There are comparatively few studies which have simultaneously measured routine respiration rate and activity. At very low swimming speeds, respiration rate has been found to be linearly (Spoor 1946) and log linearly (Smit 1965; Muir et al. 1965) related to activity. In the present study, the routine swimming speeds were clustered within a narrow range (0.36-0.59 BL/s), and there was no detectable relationship between respiration rate and swimming speed.

In all of the nonfeeding (initial, final, postfeeding) measurements, the respiration rates were higher than those which would have been predicted from the observed swimming speeds and an extrapolation of Equation (3) (Table 2, Figure 5). Thus the respiration rates of the fish when they were not feeding, and therefore swimming slowly, were higher per unit swimming speed than when the fish were feeding and swimming more rapidly. These results were consistent with previous studies, in which routine metabolic rates also tended to be variable, and elevated above those

predicted from respiration rate-swimming speed relationships during long-term swimming at constant speed (Brett 1964; Smit 1965; Muir and Niimi 1972). Explanations for this phenomenon include: 1) stress, which elevates the metabolic rate, is reduced when the fish are occupied by some activity such as swimming against a water current (Brett 1964), or feeding, if the fish are nonaggressive (this study); 2) the intermittent swimming of spontaneously active fish, accompanied by frequent accelerations and changes in direction, is hydrodynamically less efficient than the smooth caudal locomotion of continuous swimming and thus exacts a relatively higher metabolic cost (Smit 1965).

The increased respiration rates during feeding consumed a significant fraction of the energy obtained from the ration (Table 1, column 6). Energy expenditures above routine during the postfeeding period averaged 4.61% of the energy contained in the food ration (Table 1, column 9). The increased metabolic rate during and soon after feeding appeared to be primarily due to the increased voluntary swimming speed. Swimming speed accounted for 84.3% of the variability in metabolic rate during feeding and 73.3% during the postfeeding period (Table 2). Other factors which may affect the metabolic rate as a result of feeding include changes in excitability of the fish, and the calorigenic effect of the food ration (SDA, the "specific dynamic affect").

The excitability of the fish is in practice difficult to measure. Qualitative observations of the behavior of the fish and the degree of variability in their swimming behavior (Figure 3) indicated that excitability was not a significant factor contributing to the elevated respiration during feeding, but could be important during the postfeeding period of restlessness. The latter evidently resulted from the abrupt termination of the input of food when the fish were not satiated.

The cost of digestion and transformation of the food, or SDA, has generally been measured as an increase in oxygen consumption following feeding (Kleiber 1961; Warren and Davis 1967). In several earlier studies, in which fish were fed a single meal over a brief period, the increase in oxygen consumption peaked several hours after the meal, then gradually subsided over a prolonged period (as long as 2-3 d) to the prefeeding level (Muir and Niimi 1972; Pierce and Wissing 1974; Beamish 1974). In these species, digestion of the food also occurs over an extended period. The energy loss to SDA was generally estimated to represent about 12-16% of the energy content of the ration.

The Atlantic menhaden results differed considerably from these earlier studies. There was no peak in oxygen consumption during the postfeeding period, but instead a rapid and continuous return of the metabolic rate to the prefeeding level. This rapid return is consistent with the rapid digestion rates observed for menhaden.[4] Food was assimilated within 1-2 h after ingestion, and approximately 80% of the food ingested during the 7-h feeding period was digested and assimilated within the same period. The amount of energy expended above the routine during the postfeeding period was larger in the larger ration experiments (Table 1, columns 7, 8), which may appear to indicate some effect of SDA. However, voluntary activity levels were also higher in these experiments. SDA is believed to be proportional to ration size, but if the oxygen consumption attributable to swimming activity, Equation (3) (Table 2) is subtracted from the total respiration rate during the postfeeding period, there was no relationship between ration size and the amount of elevated respiration which can be ascribed to SDA.

Thus, while Atlantic menhaden may be assumed to experience some respiratory costs related to SDA, the major part of these will be included as a part of the total respiratory increase during feeding. In practice it would be very difficult to distinguish SDA in the total metabolism because of the overwhelming effect of swimming speed on the metabolic rate.

Equations (2) and (3) (Table 2) may be extrapolated to zero activity to obtain an estimate of standard metabolism. These estimates, 0.036 mg O_2/g per h from Equation (2) and 0.029 mg O_2/g per h from Equation (3) are generally lower than those reported from most other fishes which have been studied (Table 3). Respiration rates which menhaden sustained during feeding were also high relative to those which can be sustained by other species, and actually exceeded the active rate (the maximum which can be maintained for 1 h) (Brett 1964) of a number of species, including the aholehole, largemouth bass, rainbow trout, and tilapia (Table 3). Since the present study measured only voluntary respiration rates, the active

[4]Durbin, E. G., and A. G. Durbin. Assimilation efficiency and nitrogen excretion of a filter-feeding planktivore, the Atlantic menhaden *Brevoortia tyrannus*. Unpubl. manuscr.

TABLE 3.—Metabolic rates among 10 fish species. Except where noted, rates were extrapolated to a 300 g fish, using the appropriate weight-swimming speed-respiration relationships.

Species	Temperature (° C)	Standard mg O_2/g per h	Active mg O_2/g per h	Author
Brook trout, *Salvelinus fontinalis*	20	0.153		Beamish (1964)
White sucker, *Catostomus commersonii*	20	0.086		Beamish (1964)
Brown bullhead, *Ictalurus nebulosus*	20	0.093		Beamish (1964)
Carp, *Cyprinus carpio*	20	0.043		Beamish (1964)
Tilapia, *Tilapia nilotica*	25	0.086	0.378	Farmer and Beamish (1969)
Largemouth bass, *Micropterus salmoides*	20	~0.10	0.302	Beamish (1970)
Rainbow trout, *Salmo gairdneri*[1]	15	0.073	0.48	Webb (1971)
Aholehole, *Kuhlia sandvicensis*	23	0.043	0.387	Muir and Niimi (1972)
Sockeye salmon, *Oncorhynchus nerka*	20	0.103	0.799	Brett and Glass (1973)
Atlantic menhaden, *Brevoortia tyrannus*[1]	20	0.029	(0.538)[2]	This study

[1]Actual measured values; $\bar{x}$ wet weight of rainbow trout = 272 g, and Atlantic menhaden = 302 g.
[2]Maximum voluntary metabolic rate in this study; presumably less than active rate.

rate in menhaden remains unknown, though presumably higher than those reported here. Thus the metabolic "scope" (Fry 1947) in menhaden appears to be significantly larger than that of many species. A large metabolic scope is consistent with Hartwell and Otto's (1978) finding that the critical swimming speeds in juvenile Atlantic menhaden far exceed those reported from other species: at 20° C nonfeeding fish averaging 5.8 cm standard length were able to maintain a speed of 15.8 BL/s for 64 min and a speed of 20.8 BL/s for 2 min. In contrast, at 20° C the critical speed of a 6 cm sockeye salmon, for example, is only about 6.5 BL/s (Brett and Glass 1973).

The respiration during feeding increased significantly faster per increment in swimming speed in menhaden than in other species which have been studied. In Atlantic menhaden an increase in swimming speed of 1 BL/s caused a 5.8-fold increase in the respiration rate (Table 2, Equation (3)); while for eight species reviewed by Beamish (1978) (*Oncorhynchus nerka*, *Lepomis gibbosus*, *Melanogrammus aeglefinus*, *Tilapia nilotica*, *Micropterus salmoides*, *Liza macrolepis*, *Cyprinus carpio*, *Salmo gairdneri*), a similar increase in speed caused a roughly 2.3-fold elevation in the metabolic rate. Thus the cost of increasing the swimming speed is 2.5 times higher in Atlantic menhaden during feeding than in these eight species (which were not feeding).

The very steep slope of the swimming speed-respiration relation for the Atlantic menhaden indicates that during feeding, the loss in streamlining caused by the expanded opercula and the resistance of the closely spaced gill rakers substantially increase the hydrodynamic drag of the fish. It is likely that the respiratory cost for nonfeeding Atlantic menhaden swimming at equivalent speeds would be much lower. It would be of interest to determine the maximum swimming performance of nonfeeding adult fish, for comparison with Hartwell and Otto's (1978) data from juveniles.

The rapidly increasing respiratory cost of swimming during feeding is perhaps more clearly illustrated when the relationship is plotted arithmetically (Figure 5, inset). The highest mean voluntary swimming speed in the present experiments, 43.4 cm/s or 1.68 BL/s, is very close to the inflection of the curve in Figure 5 (inset), beyond which an increase in swimming speed drastically increases the metabolic rate. Because of the high energy cost it is likely that in nature the voluntary swimming speeds of adult Atlantic menhaden during feeding will be <2 BL/s for most of the time.

In conclusion, the Atlantic menhaden, a filter-feeding planktivore, offers an interesting contrast to pelagic predaceous fishes, which have been more widely studied (Durbin 1979). These predators typically consume their daily ration in a few large meals (they are "macrophagists"). The time and energy costs of feeding varies in different species, and the energy lost to SDA is a conspicuous component of their daily metabolism. In contrast, a "microphagist," such as the Atlantic menhaden, consumes its food as a continuous stream of very small food particles. While the energy cost associated with feeding is consistently high, in menhaden there is no extended period of elevated respiration following feeding, as observed in macrophagists, but rather a continuous and rapid return to prefeeding rates.

ACKNOWLEDGMENT

We would like to thank Harold Loftes, skipper of the *Ocean State*, and Charles Follett, skipper of the *Cindy Bett*, for their assistance in obtaining

menhaden. We also thank T. J. Smayda for the use of his laboratory facilities, and the National Science Foundation for support of this research under grant OCE 7602572.

LITERATURE CITED

BEAMISH, F. W. H.
1964. Respiration of fishes with special emphasis on standard oxygen consumption. II. Influence of weight and temperature on respiration of several species. Can. J. Zool. 42:177-188.
1970. Oxygen consumption of largemouth bass, *Micropterus salmoides*, in relation to swimming speed and temperature. Can. J. Zool. 48:1221-1228.
1974. Apparent specific dynamic action of largemouth bass, *Micropterus salmoides*. J. Fish. Res. Board Can. 31:1763-1769.
1978. Swimming capacity. *In* W. S. Hoar and D. J. Randall (editors), Fish physiology, Vol. VII, p. 101-189. Acad. Press.

BRETT, J. R.
1964. The respiratory metabolism and swimming performance of young sockeye salmon. J. Fish. Res. Board Can. 21:1183-1226.

BRETT, J. R., AND N. R. GLASS.
1973. Metabolic rates and critical swimming speeds of sockeye salmon (*Oncorhynchus nerka*) in relation to size and temperature. J. Fish. Res. Board Can. 30:379-387.

DURBIN, A. G.
1979. Food selection by plankton feeding fishes. *In* H. Clepper (editor), Predator-prey systems in fisheries management, p. 203-218. Sport Fishing Institute, Wash., D.C.

DURBIN, A. G., AND E. G. DURBIN.
1975. Grazing rates of Atlantic menhaden *Brevoortia tyrannus*, as a function of particle size and concentration. Mar. Biol. (Berl.) 33:265-277.

DURBIN, E. G.
1977. Studies on the autecology of the marine diatom *Thalassiosira nordenskioeldii*. II. The influence of cell size on growth rate, and carbon, nitrogen, chlorophyll *a* and silica content. J. Phycol. 13:150-155.

IVLEV, V. S.
1961. Experimental ecology of the feeding of fishes. Yale Univ. Press, New Haven, 302 p.

PECK, J. I.
1894. On the food of menhaden. Bull. U.S. Fish Comm. 13:113-126.

PIERCE, R. J., AND T. E. WISSING.
1974. Energy cost of food utilization in the bluegill (*Lepomis macrochirus*). Trans. Am. Fish. Soc. 103:38-45.

RICKER, W. E.
1973. Linear regressions in fishery biology. J. Fish. Res. Board Can. 30:409-434.
1975. A note concerning Professor Jolicoeur's comments. J. Fish. Res. Board Can. 32:1494-1498.

SKAZHINA, E. P.
1975. Energy metabolism of anchovy *Engraulis encrasicholus* L. when kept in a group or isolated and when anesthetized with quinaldine. Dokl. Biol. Sci. Engl. Transl. 225:557-558.

SMIT, H.
1965. Some experiments on the oxygen consumption of goldfish (*Carassius auratus* L.) in relation to swimming speed. Can. J. Zool. 43:623-633.

SPOOR, W. A.
1946. A quantitative study of the relationship between the activity and oxygen consumption of the goldfish and its application to the measurement of respiratory metabolism in fishes. Biol. Bull. (Woods Hole) 91:312-325.

STRICKLAND, J. D. H., AND T. R. PARSONS.
1972. A practical handbook of seawater analysis. Fish. Res. Board Can. Bull. 167.

WARREN, C. E., AND G. E. DAVIS.
1967. Laboratory studies on the feeding, bioenergetics, and growth of fish. *In* S. D. Gerking (editor), The biological basis of freshwater fish production, p. 175-214. Wiley, N.Y.

WEBB, P. W.
1971. The swimming energetics of trout II. Oxygen consumption and swimming efficiency. J. Exp. Biol. 55:521-540.

YENTSCH, C. S., AND D. W. MENZEL.
1963. A method for the determination of phytoplankton chlorophyll and phaeophytin by flourescence. Deep-Sea Res. 10:221-231.

USING BOX-JENKINS MODELS TO FORECAST FISHERY DYNAMICS: IDENTIFICATION, ESTIMATION, AND CHECKING

ROY MENDELSSOHN[1]

ABSTRACT

Box-Jenkins models are suggested as appropriate models for forecasting fishery dynamics. Unlike standard production models, these models are empirical, dynamic, stochastic models. Box-Jenkins models are not biased when estimating relationships between catch and effort, as are standard production models. The use of these techniques is illustrated on catch and effort data for the skipjack tuna fleet in Hawaii. An actual 12-month forecast is shown to give a reasonable fit to the observed data. Most of the discrepancies are explained by changes in the behavior of the fishermen (i.e., economic factors), rather than by lack of knowledge of the behavior of fish.

Accurate forecasting models would be useful in fishery management because extended jurisdiction and international agreements require preseasonal predictions of the actual catch of a fleet. In addition, improved forecasts of fish availability can lead to improved planning by fishermen or by processing firms. Forecasting techniques have expanded greatly in the last years, but few have been adapted to research in fisheries management. Instead, techniques designed to establish the equilibrium health of the stocks are also being used to attempt dynamic forecasting.

At present, two least squares procedures are being used to estimate the general production model, the search procedure of Pella and Tomlinson (1969) and the weighted least squares of Fox (1970, 1971, 1975). The Fox procedure fits catch per unit effort against a function of lagged effort. Several authors (Chayes 1949; Eberhardt 1970; Atchley et al. 1976) have demonstrated that scaling the dependent variable (i.e., catch) by the independent variables (i.e., effort) biases the fit by introducing artificial correlation into the data. Johnston (1972) showed that ordinary least squares gave biased estimates and an inflated F-statistic when used with variables lagged on themselves. Neither the Fox nor the Pella-Tomlinson procedure accounts for the effect of autocorrelated errors in the estimation procedure which Granger and Newbold (1977) and Newbold and Davies (1978) have demonstrated bias both estimation and tests of fit. An examination of the residuals in Fox (1971, figure 3B) clearly shows them to be autocorrelated. Residuals from many spawner-recruit curves display similar behavior.

In this paper, the use of Box-Jenkins models for modeling and forecasting fisheries dynamics is explored. Box-Jenkins and other related forecasting techniques are specifically designed for estimating and testing models in the presence of autocorrelated errors. The fitted models are stochastic rather than deterministic, thus reflecting the variability found in most fisheries. The models are constructed empirically, and are best suited for forecasting. The models tell us little about the long-term health of the stocks, so that a judicious use of production, yield per recruit, and accurate forecasting models is required to give the best overall picture of the fishery.

My preference for Box-Jenkins models over other forecasting methods now available is due to the good documentation (see for example Anderson 1975; Box and Jenkins 1976; Granger and Newbold 1977) and computer accessibility. The results presented here were obtained using a package originally developed by David Pack at Ohio State University and now available through Automatic Forecasting Systems.[2]

The three-step process of model identification, model estimation, and model diagnostic checking is illustrated by developing a model that makes monthly forecasts of skipjack tuna, *Katsuwonus pelamis*, catches in Hawaii. Experience with the model suggests that for a 12-mo forecast of catch,

[1]Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96812.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Manuscript accepted May 1980.
FISHERY BULLETIN: VOL. 78, NO. 4, 1981.

during peak months the forecast is within 15% of the observed catch (and is usually within 8-10% of the observed catch), most turning points in the catch trend are predicted, and the important feature of a low, flat catch during the summer months or high, peaked catches are accurately predicted. Moreover, the reasons for forecasts with large errors appear to be related more to fishermen's decisions in face of weather and economic factors, than to mispredicting the availability of the fish.

THE DATA AND UNDERLYING MODEL

The data to be analyzed are landings of skipjack tuna by approximately 12 boats from Oahu during 1964 through 1978. The raw data consist of the daily landings (each boat rarely stayed out more than a day or two), broken down by boat, and by four skipjack tuna size classes: large, medium, small, and extra small. For purposes of analysis, the data were aggregated into monthly totals, with the total number of fishing trips used as the measure of fishing effort. For monthly catch and effort during 1964-78 see Figures 1 and 2.

There are several causes for the observed seasonal variability. First, the tuna are only available in large numbers seasonally. Second, price considerations, particularly around Christmas and New Year when there is large demand, tend to spur fishing even when availability is low. Third, with only 12 boats fishing, if 1 or 2 boats are not able to fish for a few weeks, the catch will drop sharply. Finally, environmental factors, particularly weather (such as bad seas) will affect the landings since the boats are unable to fish.

Folklore in Hawaii has it that the catch remains similar each year, no matter how many boats fish. Comitini[3] examined the fishery using dummy variables and ordinary least squares to estimate

[3]Comitini, S. 1977. An economic analysis of the state of the Hawaiian skipjack tuna fishery. Sea Grant Tech. Rep. UNIHI-SEAGRANT-TR-78-01, 46 p.

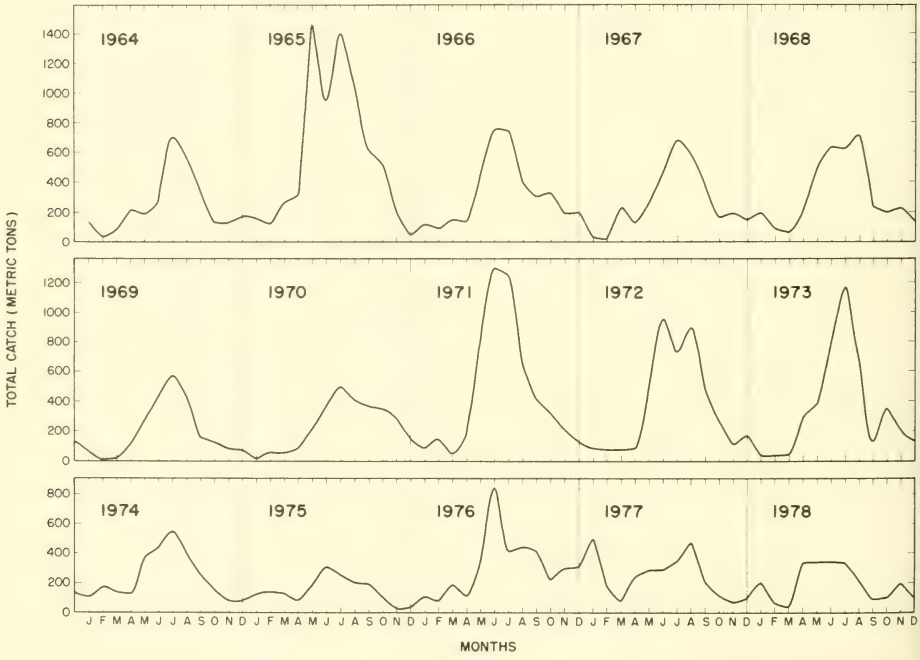


FIGURE 1.—Level of Hawaiian skipjack tuna catch by month, 1964-78.

a Cobbs-Douglas production function. He concluded, among other things, that natural fluctuations in resource availablity are significant, but did not include them in his analysis, nor did he provide a means for forecasting future catch. The National Marine Fisheries Service, using a regression model based on the previous year's catch, water temperature, and salinity at the start of the year, makes yearly predictions that have been mixed in accuracy.

Box-Jenkins models are autoregressive-integrated-moving-average models, or ARIMA models. These are linear, stochastic models that can describe fairly complex behavior, in contrast to Parrish and MacCall (1978) who use highly nonlinear equations to model the fluctuations in fishery data.

The modeling is based on the properties of stationary time series. A time series x_t is stationary if it has a constant mean, and if the covariance between events x_t, x_{t-s} depends only on s and not on t. Many series are stationary after removing a deterministic trend. Others are differenced in order to achieve stationary. Also, transforming the time series, particularly using the Box-Cox family of transformations, often improves the behavior of the time series. The initial step then is to transform and difference the data as necessary to achieve stationary. It is convenient to use the backshift operator B^j, where $B^j x_t = x_{t-j}$, to denote lagged variables. Given the new series $z_t = (1 - B^d)x_t$, a mixture of autoregressive and moving average models are sought. Autoregressive models are models that depend on the past history of the time series:

$$z_t = \phi_1 z_{t-1} + \phi_2 z_{t-2} + \ldots + \phi_p z_{t-p} + a_t$$

in terms of the backshift operator:

$$(1 - \phi_1 B - \phi_2 B^2 - \ldots - \phi_p B^p) z_t = a_t$$

while moving average models depend on past values of the noise or error:

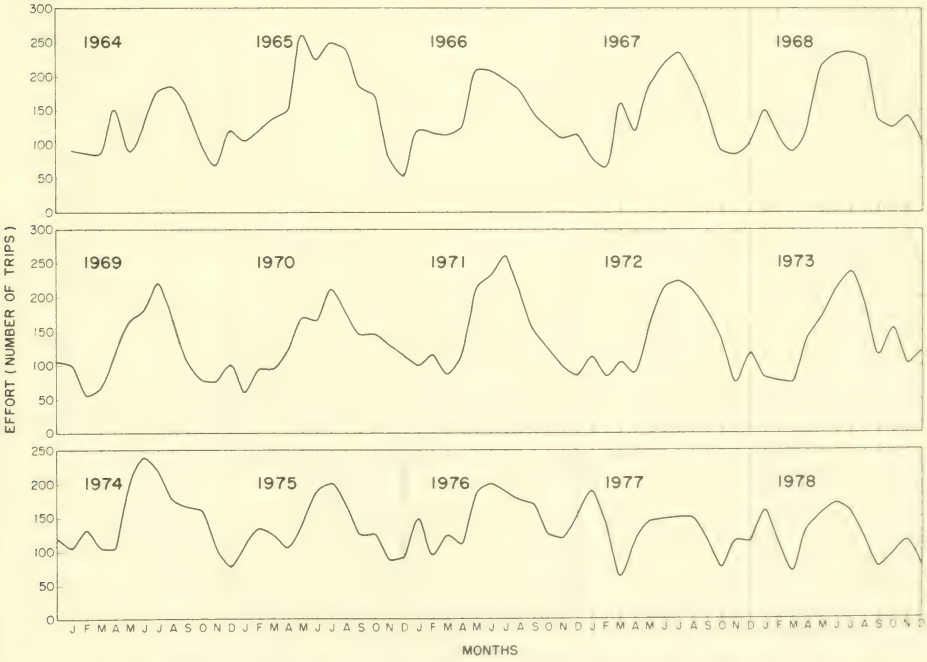


FIGURE 2.—Number of fishing trips per month by the Hawaii skipjack tuna fleet 1964-78, near Oahu, Hawaii.

$$z_t = a_t - \theta_1 a_{t-1} - \theta_2 a_{t-2} - \ldots - \theta_q a_{t-q}$$

or:

$$z_t = (1 - \theta_1 B - \theta_2 B^2 - \ldots - \theta_q B^q) a_t .$$

A model that has both moving average and autoregressive parameters is a mixed autoregressive moving average model, whose representation in terms of the backshift operator is:

$$(1 - \phi_1 B - \phi_2 B^2 - \ldots - \phi_p B^p)(1 - B)^d x_t$$

$$= (1 - \theta_1 B - \theta_2 B^2 - \ldots - \theta_q B^q) a_t .$$

MODEL IDENTIFICATION

The first step in the Box-Jenkins modeling process is to use properties of the data to tentatively identify a model. Even if a multivariate model (i.e., a model based on catch and effort) is the ultimate goal, univariate models of each series are constructed first. Often the univariate model produces forecasts that are almost as accurate as the multivariate model forecast.

My procedure was to identify, estimate, and check a series of models based on the data from January 1964 through July 1977. These models were used to forecast the already observed catch and effort for the period August 1977-December 1978. The models with the best "fit" were then reestimated to make the forecast for 1979. To make clear the feedback nature of identification, estimation, and checking in Box-Jenkins models, results from models fixed to 163 and 180 mo of data are intermingled, but clearly labeled.

A tentative model can be identified by estimating the autocorrelation and partial autocorrelation functions for each series. These are shown in Figures 3 and 4. Significant is the undamped sinusoidal behavior of each, with a period of 12 mo. Failure of both the autocorrelation and partial autocorrelation functions to go to zero is a sign of a nonstationary series, and the need for differencing. The 12-mo period suggested a yearly seasonal model, so that twelfth differences were taken, i.e., $z_t = (1 - B^{12}) x_t$.

The estimated autocorrelation and partial autocorrelation functions for the differenced catch and effort series are given in Tables 1 and 2. Following guidelines in appendix 9.1 in Box and Jenkins (1976), seasonal models with period s of the form:

$$z_t = (1 - \theta_1 B - \theta_2 B^2)(1 - \Theta_1 B^s) a_t \qquad (1a)$$

or $z_t = (1 - \theta_1 B - \theta_2 B^2)$

$$(1 - \Theta_1 B^s - \Theta_2 B^{2s}) a_t \qquad (1b)$$

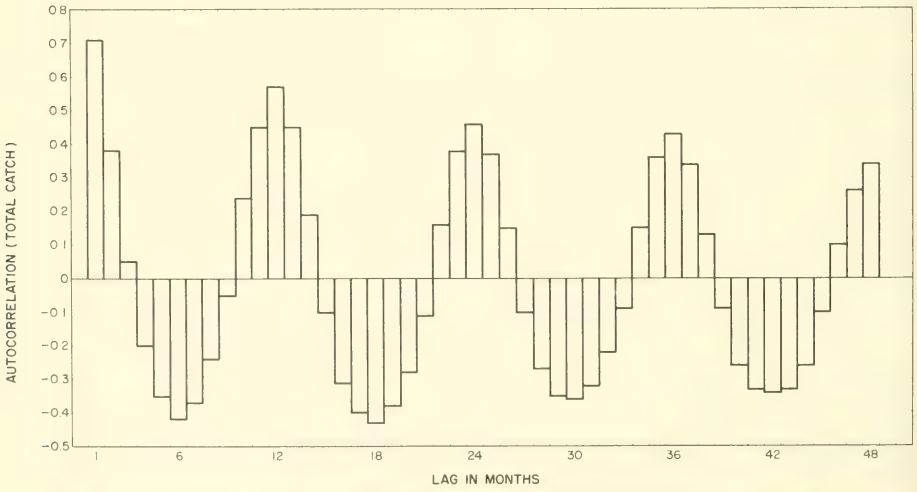


FIGURE 3.—Estimated total catch autocorrelation function for the catch of skipjack tuna near Oahu, Hawaii, 1964-78.

TABLE 1.—Autocorrelation functions for 12th differenced effort series of the Hawaii skipjack tuna fleet, 1964-78.

Item	Lag (mo) 1	2	3	4	5	6	7	8	9	10	11	12	13	14
Regular auto.	0.39	0.17	0.20	0.16	0.10	0.04	0.03	0.07	−0.02	−0.08	−0.20	−0.45	−0.18	−0.08
SE	08	09	.10	10	10	10	10	.10	.10	.10	.10	.10	12	12
Partial auto.	.39	.03	.15	03	01	−.04	00	00	−.08	−.07	−.19	−.39	15	04

Item	Lag (mo) 15	16	17	18	19	20	21	22	23	24	25	26	27
Regular auto.	−0.18	−0.13	−0.12	−0.17	−0.15	−0.17	−0.12	0.05	0.04	0.02	0.00	−0.07	0.03
SE	.12	12	12	.12	.12	.12	13	13	13	13	.13	13	13
Partial auto.	−.03	02	−.07	−.14	−.01	−.02	−.05	.16	−.08	−.19	.05	−.12	03

TABLE 2.—Autocorrelation functions for 12th differenced catch series of the Hawaii skipjack tuna fleet, 1964-78.

Item	Lag (mo) 1	2	3	4	5	6	7	8	9	10	11	12	13	14
Regular auto	0.58	0.40	0.33	0.20	0.11	0.05	0.01	0.02	−0.06	−0.12	−0.21	−0.38	−0.21	−0.15
SE	08	.11	12	12	.12	.12	.12	.12	.12	.12	.13	.13	.14	.14
Partial auto.	.58	09	10	−.07	−.03	−.04	−.00	04	−.11	−.07	−.17	−.29	28	03

Item	Lag (mo) 15	16	17	18	19	20	21	22	23	24	25	26	27
Regular auto.	−0.16	−0.12	−0.08	−0.09	−0.08	−0.12	−0.10	−0.08	−0.08	−0.09	−0.06	−0.06	−0.05
SE	.14	.14	.14	.14	.14	14	.14	.14	.14	.14	.14	.14	.14
Partial auto.	−.01	−.06	02	−.07	02	−.05	−.04	−.04	−.11	−.17	−.19	−.01	−.02

were hypothesized as the appropriate univariate models for both the catch and the effort time series.

ESTIMATION AND CHECKING

Given a tentative model, such as Model (1), the next step is a recursive procedure of estimating the parameters of the model, calculating the autocorrelation and partial autocorrelation functions of the residuals from the estimated model, and then testing the residuals for significant departure from the assumption that they are white noise. When a final model has been identi-

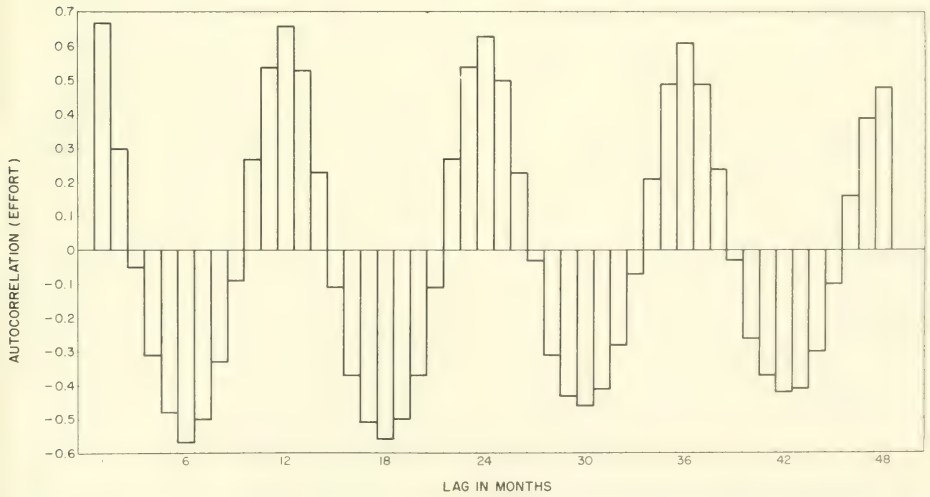


FIGURE 4.—Estimated effort autocorrelation function for the fishing trips by the Hawaii skipjack tuna fleet near Oahu, Hawaii, 1964-78.

fied, overfitting is tried, that is extra parameters are added to see if they are found to be not significantly different from zero.

To insure that I found the simplest model possible, I fitted first the model $z_t = (1 - \theta_1 B)(1 - \Theta_1 B^{12})a_t$, and then added parameters as seemed necessary based on the diagnostic checking. The estimates for Model (1) for catch and effort are given in Tables 3 and 4. Estimates using two estimation techniques, one using backforecasting and one suppressing it, are presented. Some programs do not have a backforecasting feature; my experience is that the estimated models obtained using backforecasting are far superior, as can be seen in the tables presented.

TABLE 3.—Parameter estimates for effort model, Model (1) (see text). (Based on 180 observations.)

Parameter	Estimate supressing backforecasting	SE	Estimate using backforecasting	SE
θ_1	−0.38349	0.07942	−0.44756	0.07886
θ_2	−.11326	07996	−.12795	.07911
Θ_1	.5894	.08122	.99493	.00650
Θ_2	.00069	.08609	—	—
χ^2 statistic on residuals	26.894 with 44 df		37.319 with 45 df	
Residual mean square	1,018.60		755.270	
Residual SE	31.915		27.482	
Residual mean	1.629		0.5338	

TABLE 4.—Parameter estimates for catch model, Model (1) (see text). (Based on 163 observations.)

Parameter	Estimate suppressing backforecasting	SE
θ_1	−0.54100	0.08190
θ_2	−.22745	.08235
Θ_1	.75314	.08718
Θ_2	05184	.09256
χ^2 statistic on residuals	27.470 with 43 df	
Residual mean square	165.410	
Residual SE	406.71	
Residual mean	17.506	

The estimated autocorrelation and partial autocorrelation functions of the residuals from both models are given in Tables 5 and 6. For the effort series, there is no sign of a lack of fit, while for the catch series terms of lag three or four are suggested. An overspecified model:

$$z_t = (1 - \theta_1 B^1 - \theta_2 B^2 - \theta_3 B^3 - \theta_4 B^4)(1 - \Theta_1 B^{12})a_t \quad (2)$$

was estimated for both the catch and effort time series. The results are summarized in Tables 7 and 8. The estimated autocorrelation and partial autocorrelation functions of the residuals (not shown) show no sign of additional lags or trend. The test statistic that the residual series are not significantly different from white noise gave no reason to doubt the models adequacy, and overfitting by including a $\Theta_2 B^{24}$ term found this term to be nonsignificant.

TRANSFER FUNCTION MODELS

If both the catch time series, say y_t, and the effort time series, say x_t, have been suitably transformed so that the resulting series are stationary, a transfer function of the form:

$$(1 - \delta_1 B - \delta_2 B^2 - \ldots - \delta_r B^r)x_t = (\omega_0 - \omega_1 B - \omega_2 B^2 - \ldots - \omega_s B^s)y_{t-b} + \eta_t$$

can be estimated where η_t is not assumed to be white noise, but itself can be modeled as an autoregressive-moving average process of a_t.

The procedures for identifying and estimating a transfer function model are similar to those for the univariate model, except that attention is focused on the estimated cross-correlation function between the "prewhitened" catch and effort series. Series are prewhitened if they are reduced to the residuals left from a given model. In this instance, both series are prewhitened by the univariate model for effort estimated in the preceding section. The estimated correlation function, impulse response function, and residual noise autocorrelation function are given in Table 9. The estimated autocorrelation function for the noise is similar to the original univariate autocorrelations, suggesting a noise model of the form:

$$\eta_t = (1 - \theta_1 B - \theta_2 B^2 - \theta_3 B^3 - \theta_4 B^4)(1 - \Theta_1 B^{12})a_t. \quad (3)$$

Based on guidelines in Box and Jenkins (1976:386-388) and knowledge of the fishery, two models were hypothesized:

$$(1 - B^{12})y_t = (\omega_0)(1 - B^{12})x_t + \eta_t \quad (4)$$

and: $(1 - \delta_1 B - \delta_2 B^2)(1 - B^{12})y_t = (\omega_0 - \omega_1 B - \omega_2 B^2)(1 - B^{12})x_t + \eta_t$. (5)

Tables 10 and 11 summarize the estimates when

TABLE 5.—Estimated autocorrelation function for residuals of effort model for the Hawaii skipjack tuna fleet, 1964-78.

Item	Lag (mo) 1	2	3	4	5	6	7	8	9	10	11	12
Auto.	0.01	0.03	0.09	0.06	0.04	−0.11	−0.05	0.04	−0.09	0.02	0.03	−0.01
SE	.07	.07	.07	.08	.08	.08	.08	.08	.08	.08	.08	.08
Item	Lag (mo) 13	14	15	16	17	18	19	20	21	22	23	24
Auto.	0.05	−0.01	−0.04	−0.09	−0.08	−0.09	−0.07	−0.08	−0.16	0.10	0.07	−0.02
SE	.08	.08	.08	.08	.08	.08	.08	.08	.08	.08	.08	.08

TABLE 6.—Estimated autocorrelation function for residuals of catch model for the Hawaii skipjack tuna fleet, 1964-78.

Item	Lag (mo) 1	2	3	4	5	6	7	8	9	10	11	12
Auto.	0.04	0.11	0.23	0.06	0.06	−0.05	0.00	0.10	−0.03	0.04	0.01	0.00
SE	.08	.08	.08	.09	.09	.09	.09	.09	.09	.09	.09	.09
Item	Lag (mo) 13	14	15	16	17	18	19	20	21	22	23	24
Auto.	0.05	−0.01	−0.07	−0.01	−0.00	−0.04	0.00	−0.01	−0.06	0.01	−0.04	−0.03
SE	.09	.09	.09	.09	.09	.09	.09	.09	.09	.09	.09	.09

backforecasting is used in estimating the parameters for Models (4) and (5). The chi-square statistics show no reason to suspect model inadequacy. The residuals show no significant cross-correlation with total catch, when $1/\sqrt{180}$ (180 observations in the series) is used as a rough standard error. The residual autocorrelation function shows spikes around lag 15 that are higher than would be desired, but overall the fit is reasonable, and the model residuals could reasonably be modeled as white noise.

TABLE 7.—Parameter estimates for effort model, Model (2) (see text). (Based on 180 observations.)

Parameter	Estimate suppressing backforecasting	SE	Estimate using backforecasting	SE
θ_1	−0.36746	0.08004	−0.43862	0.07930
θ_2	−.14976	.08412	−.18144	.08590
θ_3	−.16111	.08458	−.15377	.08617
θ_4	−.17096	.08454	−.16298	.08593
θ_5	−.11547	.08089	−.17291	.07998
Θ_1	.59065	.06431	.99483	.00033
χ^2 statistic on residuals	20.696 with 42 df		27.494 with 42 df	
Residual mean square	1,000.40		752.67	
Residual SE	31.629		27.435	
Residual mean	.82151		.35175	

TABLE 8.—Parameter estimates for catch model, Model (2) (see text). (Based on 180 observations.)

Parameter	Estimate suppressing backforecasting	SE	Estimate using backforecasting	SE
θ_1	−0.55368	0.07972	−0.53771	0.07462
θ_2	−.35882	.08989	−.43825	.07543
θ_3	−.33817	.09056	−.41197	.01144
θ_4	−.24282	.09012	−.30909	.07479
θ_5	−.12294	.07994	−.14974	.07440
Θ_1	.76951	.05062	.99585	.00825
χ^2 statistic on residuals	15.092 with 42 df		20.384 with 42 df	
Residual mean square	143.240		115.170	
Residual SE	378.47		339.37	
Residual mean	2.1150		3.3299	

DISCUSSION AND FORECASTS

Two transfer function models and one univariate model have been used to forecast the catch and effort in the skipjack tuna fishery during 1979. It is worth emphasizing that the original 12-mo forecasts were made in January 1979 and the updated forecasts were made in May 1979, so the reported results are true forecasts—there was no a priori knowledge of the data to help improve the "fit" of the forecasts. The original catch and effort forecasts are given in Tables 12 and 13 while the updated catch forecasts are given in Table 14.

The models used to produce the forecasts are best understood when written out in difference equation form. The univariate model for catch is:

$$y_t = y_{t-12} + (a_t + 0.538a_{t-1} + 0.438a_{t-2} + 0.412a_{t-3} + 0.309a_{t-4}) \quad (6)$$

$$- (0.996a_{t-12} + 0.535a_{t-13} + 0.436a_{t-14} + 0.410a_{t-15} + 0.308a_{t-16}),$$

i.e., catch this month is equal to the catch during the same month last year, adjusted by a difference of the weighted sums of the forecasting errors over the previous 4 mo. If the forecasts this year have consistently underpredicted compared with last year's forecasts, then the estimated catch is increased, while if the forecasts this year have consistently overpredicted compared with last year's forecasts, then the estimated catch is decreased. The forecast maintains a balance between keeping the catch in equilibrium and keeping the error in equilibrium.

This impression of a yearly cycle with variability is reinforced when examining the polynomial

TABLE 9.—Estimated cross-correlation function, impulse response function, and noise autocovariance function for a catch-effort transfer model for the Hawaii skipjack tuna fleet, 1964-78.

Lag (mo)	Estimated cross-correlation	Estimated noise autocovariance	SE	Estimated impulse response weights
0	0.651	—		8.409
1	.080	0.49	0.10	1.035
2	.070	.21	.12	.903
3	.086	.16	.12	1.111
4	−.033	.16	.13	−.431
5	.044	.10	.13	.566
6	−.098	.07	.13	−1.269
7	.099	.03	.13	1.276
8	.103	.13	.13	1.334
9	−.017	.14	.13	−.215
10	.043	−.05	.13	.556
11	−.040	−.14	.13	−.517
12	−.20	−.26	.13	−1.555
13	.026	−.05	.14	.338
14	−.109	.05	.14	−1.404
15	.003	−.12	.14	−.038
16	−.098	−.16	.14	−.415
17	.014	−.01	.14	.043
18	−.110	−.05	.14	−1.271
19	−.037	−.12	.14	.185
20	.006	−.12	.14	−1.422
21	−.006	−.16	.14	−.475
22	−.108	−.11	.14	.080
23	.012	−.18	.15	−.075
24	−.108	−.21	.15	−1.393
25	−.001	−.09	.15	.181
26	−.108	−.08	.15	−1.390

TABLE 10.—Parameter estimates for transfer model, Model (4) (see text). (Based on 180 observations.)

Parameter	Estimate suppressing backforecasting	SE	Estimate using backforecasting	SE
ω_0	7.5989	0.69403	8.0003	0.83561
θ_1	−.47621	07993	−.48894	.07851
θ_2	−.32874	.08734	−.32633	.08541
θ_3	−.17034	.08803	−.14853	.08666
θ_4	−.20033	07905	−.17506	.07822
Θ_1	.83384	05271	.99587	.00707
χ^2 statistic on residuals	34.953 with 43 df		32.018 with 43 df	
Residual mean square	83,323		71,300	
Residual SE	288.66		267.02	
Residual mean	−15.152		0.18650	

TABLE 11.—Parameter estimates for transfer model, Model (5) (see text). (Based on 180 observations.)

Parameter	Estimate suppressing backforecasting	SE	Estimate using backforecasting	SE
δ_1	0.01286	0.30389	0.86672	0.22308
δ_2	.88121	28641	−.70763	21659
ω_0	7.3488	73352	8.1855	.82832
ω_1	−1.3011	2.16847	6.7421	1.71214
ω_2	6.8509	2.34577	−7.3133	1.58459
θ_1	−.49924	08302	−.46980	08013
θ_2	−.29495	09102	−.33234	08870
θ_3	−.16384	09191	−.17199	09012
θ_4	−.13639	08352	−.21746	08098
Θ_1	.83311	.05511	.99543	.00623
χ^2 statistic on residuals	33.067 with 43 df		38.906 with 43 df	
Residual mean square	85,673		69,066	
Residual SE	292.70		262.80	
Residual mean	−1.9979		−2.4666	

TABLE 12.—Catch forecasts for 1979 for the Hawaii skipjack tuna fleet from Models (1), (4), and (5) (see text).

Month	Model (4)	Model (5)	Model (1)	Observed catch
Jan.	102.24	157.48	159.97	52.6488
Feb.	78.91	123.32	117.81	74.1184
Mar.	121.86	118.83	108.40	102.4088
Apr.	202.05	169.75	175.82	131.0658
May	423.40	406.87	423.95	470.5450
June	595.39	605.68	598.17	358.5100
July	666.16	684.99	607.07	600.6930
Aug.	528.09	535.73	523.14	600.5200
Sept.	297.96	294.92	291.97	148.3070
Oct.	224.28	216.64	222.96	79.3360
Nov.	173.99	168.83	172.94	27.5084
Dec.	133.22	131.61	132.58	84.7755
Total	3,547.55	3,614.65	3,534.78	2,730.4367

TABLE 13.—Predicted and observed number of fishing trips for the Hawaii skipjack tuna fleet in 1979.

Month	Original prediction	Updated prediction	Observed
Jan	98.93		53
Feb.	97.50		75
Mar.	101.06		78
Apr.	122.30		118
May	174.00	167.71	173
June	196.16	187.36	182
July	209.37	206.14	200
Aug.	183.04	179.81	174
Sept.	139.18	138.73	84
Oct.	121.20	120.45	84
Nov.	104.23	104.83	51
Dec.	100.92	100.51	109

TABLE 14.—Updated forecasts of total catch for 1979 for the Hawaii skipjack tuna fleet.

Month	Model (4)	Model (5)	Model (1)	Observed catch
May	393.214	382.430	401.874	470.545
June	547.014	586.400	589.524	358.510
July	644.638	705.137	668.895	600.693
Aug.	500.151	527.945	521.456	600.520
Sept.	293.130	283.067	289.516	148.307
Oct.	220.557	197.953	222.806	79.336
Nov.	174.567	164.720	173.594	27.5084
Dec.	130.947	136.831	133.148	84.7755
Total	2,904.218	2,984.483	3,000.813	2,370.1949

representation of Model (1). The value of Θ_1 is nearly one. Thus the term $(1 - B^{12})$ appears on both sides of the equation, and can be cancelled. Abraham and Box (1978) showed that this is sufficient reason to suspect a deterministic cosine function trend with a moving average model around the trend. Given the high residual mean square for the model (115, 170), this latter interpretation is consistent with the folklore on the fishery—highly variable but on the average things are similar from year to year.

The first transfer function model is:

$$y_t = 8.003x_t + (y_{t-12} - 8.003x_{t-12}) + (a_t + 0.489a_{t-1} + 0.326a_{t-2} + 0.149a_{t-3} + 0.175a_{t-4}) \quad (7)$$
$$- (0.996a_{t-12} + 0.487a_{t-13} + 0.325a_{t-14} + 0.148a_{t-15} + 0.174a_{t-16}).$$

This model has an interpretation similar to that of the univariate model, except now catch per weighted units of effort are compared between years. The second transfer function model compares lagged values of catch and effort also.

It is difficult to judge the value of a forecast, since this will depend on the use being made of the forecast and the alternatives available. Granger and Newbold (1977) suggested the most appropriate measure of the value of a forecast is a loss function which reflects the loss from inaccurate forecast in the actual application for which the forecasts were developed. For forecasting the skipjack tuna fishery in Hawaii, there were four immediate goals. The first was to give a reasonably accurate estimate of total catch over the year, within a 15-20% error rate. The second was to predict what kind of summer it would be, May through September being the main fishing months. This means predicting what month the fish start running, what month the fish stop running, and whether the catch is high and peaked as in 1979, or flat and low as in 1978. An important concern is the relative size of the drop in catch when it occurs in September or October.

A third concern was an accurate forecast of the catch in December, when the holiday demand for sashimi (a Japanese raw fish delicacy) drives prices very high. And finally, an increased understanding of the dynamics of the fishery was desired.

Based on these criteria, I feel the forecasts have performed well, especially compared with any alternative available. The error in predicting the 1979 total catch is higher than desired. However, for the last 6 mo of 1977 the model forecasted within 8% of the observed total catch, and for the period July 1977-December 1978 the model forecasted within 12% of the observed total catch.

Except for June 1979, the summer months were predicted accurately. Experience with the model on the data from July 1977 suggests that the summer months are almost always predicted within 10% of the observed catch. In fact, in March 1979, an industry representative doubted the high catch forecasted for the summer, due to the low catch in January and February 1979. Similarly, the sharp drop in catch in September was predicted by the model. Again, in August 1979 an industry representative doubted that a sharp decline in catch would occur in September, but said that this could be a useful piece of knowledge since their decisions would change if they knew they could expect the supply to drop sharply.

The forecasts have provided insight into the fishery. The major failures of the forecasts were January 1979 and October-December 1979. January 1979 was a period of unusually bad storms, so that few fishing trips were made. However, the observed catch per trip was 0.993 metric tons (t), while Model (4) predicted a catch per trip of 1.033 t. The main source of the error in the forecast was the predicted number of trips to be made.

Similarly, the high summer catches, coupled with very high catches of yellowfin tuna, drove the price for skipjack tuna to very low levels. At the end of September, most of the boats went into drydock because of the prevailing low prices. The few boats that remained tended not to be the industry leaders (i.e., boats with a proven record of higher catch rates), and made only short forays rather than their usual fishing trips.

The point of these explanations is that the causes of the poor forecasts appear to be related not to the behavior of the fish stocks but rather to the behavior of the fishermen. Therefore, the effort to improve the forecasts needs to be directed at understanding the fishery, rather than the fish. (An economic study of the industry is near completion.)

Finally, water temperature and salinity data for one location off Oahu were included in the transfer function models. These variables added little to the forecasts, and since there is no

mechanistic explanation as to why these variables should affect the catch and effort, they are not being used at this time in the forecasts. (However, the ability to include random environmental factors into the forecasting model is an advantage when using stochastic models as compared with the normal deterministic production models.) Disaggregating by size class might also improve the forecasts. Prior to 1973, the catch of the large skipjack tuna and the total catch were highly correlated. Since 1973, this has not been true and there has been a definite change in the size composition of the catch. A disaggregated intervention model may be able to explain this change.

SUMMARY

Box-Jenkins models have been proposed as an alternate model for forecasting fishery data. ARIMA models provide maximum likelihood estimators that are not biased when the data is seasonal and autocorrelated, and when a variable is lagged on itself. Techniques are explored which allow the model to be constructed from the data up, rather than from theoretical models that may not be supported by the data. The procedure is illustrated on skipjack tuna catches in Hawaii, which traditionally has been considered too variable to forecast on a monthly basis in a reasonable manner.

ACKNOWLEDGMENTS

I am indebted to Lisa Katekaru for her invaluable assistance in performing most of the programming for this paper. Robin Allen and two anonymous referees provided several comments that have improved the presentation and discussion of this paper.

LITERATURE CITED

ABRAHAM, B., AND G. E. P. BOX.
1978. Deterministic and forecast-adaptive time-dependent models. Appl. Stat. 27:120-130.

ANDERSON, O. D.
1975. Time series analysis and forecasting: The Box-Jenkins approach. Butterworths, Lond., 182 p.

ATCHLEY, W. R., C. T. GASKINS, AND D. ANDERSON.
1976. Statistical properties of ratios: I. Empirical results. Syst. Zool. 25:137-148.

BOX, G. E. P., AND G. M. JENKINS.
1976. Time series analysis: forecasting and control. Rev. ed. Holden-Day, San Franc., 575 p.

CHAYES, F.
1949. On ratio correlation in petrography. J. Geol. 57: 239-254.

EBERHARDT, L. L.
1970. Correlation, regression, and density dependence. Ecology 51:306-310.

FOX, W. W., JR.
1970. An exponential surplus-yield model for optimizing exploited fish populations. Trans. Am. Fish. Soc. 99: 80-88.
1971. Random variability and parameter estimation for the generalized production model. Fish. Bull., U.S. 69: 569-580.
1975. Fitting the generalized stock production model by least-squares and equilibrium approximation. Fish. Bull., U.S. 73:23-37.

GRANGER, C. W. J., AND P. NEWBOLD.
1977. Forecasting economic time series. Acad. Press, N.Y., 333 p.

JOHNSTON, J.
1972. Econometric methods. 2d ed. McGraw-Hill, N.Y., 437 p.

NEWBOLD, P., AND N. DAVIES.
1978. Error mis-specification and spurious regressions. Int. Econ. Rev. 19:513-519.

PARRISH, R. H., AND A. D. MACCALL.
1978. Climatic variation and exploitation in the Pacific mackerel fishery. Calif. Dep. Fish Game, Fish Bull. 167, 110 p.

PELLA, J. J., AND P. K. TOMLINSON.
1969. A generalized stock production model. Inter-Am. Trop. Tuna Comm., Bull. 13:419-496.

DEVELOPMENT OF LARVAL SMOOTH FLOUNDER, *LIOPSETTA PUTNAMI*, WITH A REDESCRIPTION OF DEVELOPMENT OF WINTER FLOUNDER, *PSEUDOPLEURONECTES AMERICANUS* (FAMILY PLEURONECTIDAE)[1]

WAYNE A. LAROCHE[2]

ABSTRACT

Larval development is described for the first time for *Liopsetta putnami* and redescribed for *Pseudopleuronectes americanus* (Pleuronectidae). These species cooccur as larvae in Gulf of Maine estuaries during the spring and have previously been difficult to separate, especially as small larvae, due to their similar development and the lack of adequate published descriptions. Characters which distinguish *L. putnami* from *P. americanus* larvae include: presence of darkly pigmented eyes in yolk-sac larvae; lack of internal melanophores over the notochord in larvae greater than 3.2 mm; lack of melanophores on the fins of yolk-sac, preflexion, and flexion larvae; and higher ratio of snout to anus length standard length (averages 43.6 and 41.2% standard length for yolk-sac and preflexion larvae versus 33.3 and 37.6% standard length for yolk-sac and preflexion larval *P. americanus*).

The smooth flounder, *Liopsetta putnami* (Gill), Family Pleuronectidae, occurs in the western North Atlantic Ocean from Ungava Bay, Quebec, to Providence, R.I. It is found chiefly over muddy bottoms in estuaries and nearshore, marine waters <10 m deep (Bigelow and Schroeder 1953; Leim and Scott 1966). The winter flounder, *Pseudopleuronectes americanus* (Walbaum), Family Pleuronectidae, occurs from Battle Harbour and Windy Tickle, Labrador (lat. 55°45′ N), to Georgia. It is caught over hard bottoms to depths of ≈142 m on the offshore fishing banks and also in estuaries and nearshore, marine waters (Bigelow and Schroeder 1953; Leim and Scott 1966). From Providence, R.I., northwards, *L. putnami* and *P. americanus* cooccur in shallow coastal and estuarine waters where both are known to spawn (Bigelow and Schroeder 1953).

Previously, two large larvae and one small juvenile *L. putnami* have been illustrated and described (Laszlo 1972), while larval and juvenile *P. americanus* have been illustrated and their development briefly described in various publications (Sullivan 1915; Breder 1923; Bigelow and Welsh 1925; Bigelow and Schroeder 1953; Scotton et al. 1973; Lippson and Moran 1974; Klein-MacPhee 1978; Martin and Drewry 1978; and others). However, existing descriptions of *P. americanus* do not accurately present all characters necessary for reliable separation of small larvae when the species cooccur.

This paper describes the larval development of *L. putnami* for the first time from reared and field-collected specimens, redescribes the larval development of *P. americanus*, and compares the two.

METHODS

Two ripe female and one ripe male *L. putnami* were collected from the cooling water intake screens of the Maine Yankee Atomic Power Plant located on Montsweag Bay, Wiscasset, Maine, on 7 February 1974. Most *L. putnami* collected on that date were spent. The ripe fish were artificially spawned, and the eggs were fertilized in the field. Eggs were kept at 5° C in darkened containers of gently aerated 23‰ salinity water, conditions approximating those at the capture site. Field-collected larvae were captured in February and March and also were reared in the laboratory. Larvae were fed field-collected plankton.

Larvae of both *L. putnami* and *P. americanus* were collected and preserved in 3-5% Formalin[3] during 1972, 1973, and 1974 from the Sheepscot

[1]Contribution No. 139 from the Ira C. Darling Center, University of Maine, Walpole, Maine. Supported in part by a contract from Maine Yankee Atomic Power Company to the Ira C. Darling Center of the University of Maine, Orono.

[2]Ira C. Darling Center, University of Maine, Walpole, Maine; present address: Gulf Coast Research Laboratory, P.O. Drawer AG, Ocean Springs, MS 39564.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Manuscript accepted April 1980.
FISHERY BULLETIN: VOL. 78, NO. 4, 1981.

and Damariscotta River estuary systems. Larvae were collected with meter nets, ½ m buoyed and anchored nets, and a small beam trawl. The smallest *L. putnami* larvae (3.1 and 3.6 mm) were hatched from the artificially spawned eggs. The 7.1 and 7.6 mm specimens were field collected as small larvae and reared in the laboratory. All other specimens in the series were field collected and preserved. The *P. americanus* series includes only field-collected specimens.

Some specimens were lightly stained with alizarin to facilitate counting of body parts. Illustrations were prepared using a camera lucida. Measurements were taken on the right side of each specimen with an ocular micrometer mounted in a dissecting microscope. Measurements taken include:

Standard length (SL) = snout tip to notochord tip preceding development of caudal fin, then to posterior margin of hypural plate.

Total length (TL) = snout tip to tip of caudal fin membrane or fin rays.

Snout to anus length = horizontal distance from snout tip to a vertical through posterior margin of large intestine at anus.

Head length (HL) = snout tip to posterior margin of otic capsule until cleithrum becomes visible (5.4 mm in *L. putnami* vs. 3.7 mm in *P. americanus*), then to the cleithrum; to the posterior margin of the operculum on postflexion larvae >7.0 mm of both species.

Snout length = snout tip to anterior margin of orbit of right eye.

Upper jaw length = snout tip to posterior margin of maxillary.

Eye diameter = greatest width of right eye.

Body depth at pectoral fin base = vertical distance across body at pectoral fin base, not including depth of dorsal fin pterygiophores.

Maximum body depth at pectoral fin base = vertical distance across body at pectoral fin base including depth of dorsal fin pterygiophores.

Body depth behind anus = vertical distance across body immediately posterior to anus, not including depth of dorsal fin pterygiophores.

Maximum body depth behind anus = vertical distance across body immediately posterior to anus including depth of dorsal fin pterygiophores.

Pectoral fin length = distance from base to tip of fin fold or longest fin ray.

Pectoral fin base depth = width of base of pectoral fin.

Pelvic fin length = distance from insertion of pelvic fin to tip of fin fold or longest ray.

Vertebral and fin ray counts were made on juveniles with the aid of radiographs. All length measurements are standard length unless otherwise stated.

TERMINOLOGY

Yolk-sac larva = prior to absorption of yolk material.

Preflexion larva = prior to notochord flexion.

Flexion larva = undergoing notochord flexion from time urostyle begins to slant upward until urostyle is in final upturned position and caudal fin is formed.

Postflexion larva = from alignment of urostyle in final upturned position and caudal fin formation until attainment of adult dorsal and anal fin complements.

Transforming larva = from onset of migration of left eye, development of juvenile pigment pattern, and change in behavior from pelagic swimming to benthic habit until completion of these processes and attainment of adult pelvic and pectoral fin ray complements.

IDENTIFICATION

Liopsetta putnami and *P. americanus* are the only Gulf of Maine flatfishes that commonly are found in estuaries and that spawn during late winter-early spring (Bigelow and Schroeder 1953). American plaice, *Hippoglossoides platessoides*, and Atlantic halibut, *Hippoglossus hippoglossus*, also spawn during late winter-early spring but rarely enter Gulf of Maine estuaries (Bigelow and Schroeder 1953). Larval *Hippoglossoides platessoides* were described by Bigelow and Schroeder (1953) and have three vertical bands of melanistic pigment across the postanal region. Martin and Drewry (1978) compiled and summarized descriptions of larval *Hippoglossus hippoglossus* which lack vertical bands of melanistic pigment across the postanal region and hatch at lengths >8 mm. All yolk-sac larvae collected from Montsweag Bay during March had a single vertical band of melanistic pigment across the postanal region and were <5.2 mm long.

Since *L. putnami* spawns from December through February while *P. americanus* spawns from March through May and eggs take 2 or 3 wk

to hatch (Bigelow and Schroeder 1953), larval flounders collected from Montsweag Bay in early March 1974 were tentatively identified as *L. putnami*. Yolk-sac larvae hatched from artificially spawned *L. putnami* eggs appeared identical to the field-collected larvae. Since the artificially spawned larvae were few and did not live beyond yolk absorption, larvae were collected from Montsweag Bay and reared in the laboratory to verify the identification. These larvae attained the adult dorsal and anal fin ray complement of *L. putnami* during the postflexion stage, verifying the identification. In April 1974, small yolk-sac flounder larvae matching descriptions of *P. americanus* (Martin and Drewry 1978) appeared in plankton samples collected from Montsweag Bay. Two of these larvae were reared in the laboratory to the postflexion stage and attained the adult dorsal and anal fin ray complements of *P. americanus*.

Counts that identify *L. putnami* and *P. americanus* (34-38 and 34-40 vertebrae, 48-60 and 60-76 dorsal fin rays, and 34-41 and 44-58 anal fin rays, respectively) were compiled from Jordan and Evermann (1898), Norman (1934), Bigelow and Schroeder (1953), Leim and Scott (1966), and this study.

LABORATORY OBSERVATIONS

Fertilized *L. putnami* eggs were nonadhesive and demersal in 23‰ water. Eggs ranged in diam-

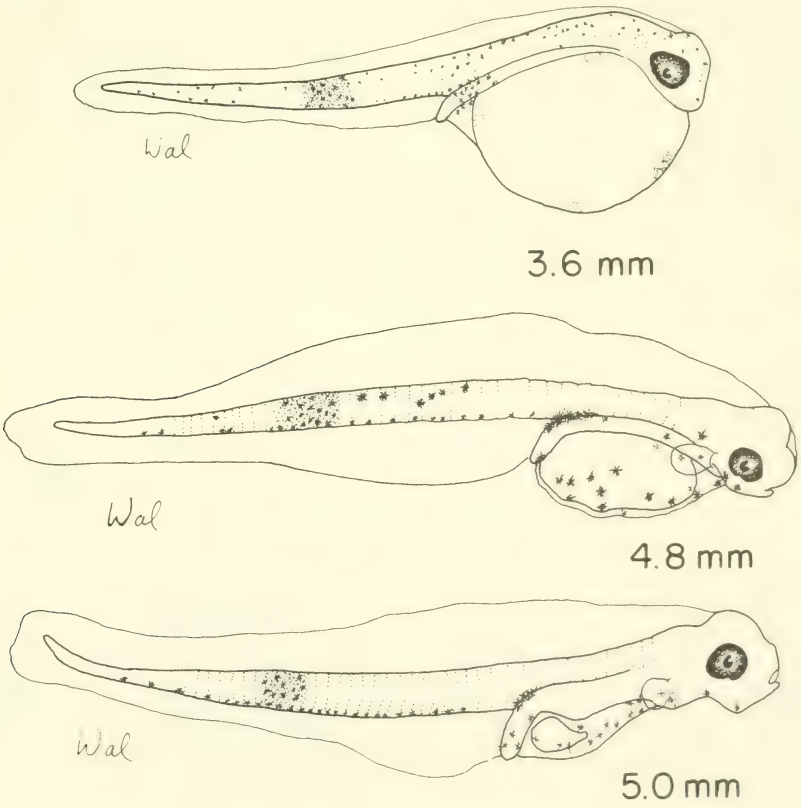


FIGURE 1.—Yolk-sac larvae of *Liopsetta putnami*.

eter from 1.1 to 1.4 mm, averaging 1.2 mm. Yolk diameter ranged from 0.9 to 1.2 mm, averaging 1.1 mm. No oil globules were obvious in newly fertilized eggs. At 5° C hatching began on the 25th day after fertilization. Newly hatched larvae were 3.1-3.6 mm long.

DISTINGUISHING FEATURES

Characters useful to distinguish larval *L. putnami* and *P. americanus* from other Gulf of Maine flatfishes are: number of myomeres, 34-38 and 38-40; hatching length, 3.1-3.6 mm and ≈2.4 mm; number of dorsal fin rays, 48-60 and 60-76; number of anal fin rays, 34-41 and 44-58; and presence of a single vertical band of melanistic pigment across the postanal region of both species.

Characters useful to distinguish yolk-sac larvae of *L. putnami* from *P. americanus* are: percentage snout to anus length/standard length, averaging 43.6% vs. 33.3%; presence of eye pigment at hatching vs. absence of eye pigment at hatching; length at hatching, 3.1-3.6 mm vs. ≈2.4 mm; and length at yolk-sac resorption, ≈5.2 mm vs. ≈3.7 mm.

Characters useful to distinguish larval *L. putnami* from *P. americanus* are: absence of internal melanophores over the notochord vs. presence of internal melanophores over the notochord; length at which gut loops, ≈5.5 mm vs. ≈4.3 mm; and absence vs. presence of anal fin pigmentation in specimens <6.3 mm.

GENERAL DEVELOPMENT
(Figures 1-8)

Reared *L. putnami* were 3.1-3.6 mm long at hatching. The smallest field-collected *L. putnami* larvae were ≈3.5 mm long. Newly hatched field-collected *P. americanus* larvae were ≈2.4 mm long. The yolk sac is resorbed by ≈5.2 and ≈3.7 mm in *L. putnami* and *P. americanus*. The gut loops by ≈5.5 mm in *L. putnami* and between 4.2 and 4.4 mm in *P. americanus*. The notochord begins to flex in *L. putnami* and *P. americanus* at ≈6.0 and ≈5.0 mm;

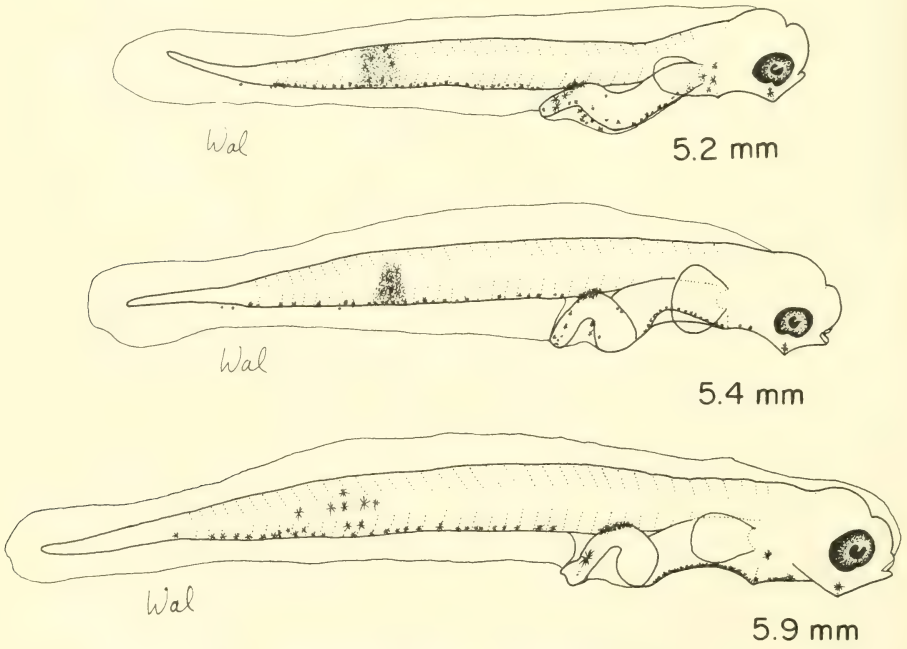


FIGURE 2.—Preflexion larvae of *Liopsetta putnami*.

flexion is completed by ≈7.1 and ≈6.6 mm; and the free tip of the notochord disappears by 7.6 and 7.3 mm. Transition from pelagic to benthic habit occurs at ≈7.3 mm in *L. putnami*. The largest pelagic field-collected *L. putnami* larva was 7.3 mm, and the largest specimen, 7.6 mm, had assumed the benthic habit in the laboratory. Transition from pelagic to benthic habit usually occurs between 6.0 and 7.0 mm in *P. americanus*. The smallest benthic-collected *P. americanus* was 5.7 mm, and the largest pelagic-collected larva was 7.4 mm long. Formation of pectoral and pelvic fin rays is completed between 8.5 and 13.0 mm (Laszlo 1972) in *L. putnami* and by ≈13 mm in *P. americanus*, marking the end of the transformation and beginning of the juvenile period.

MORPHOLOGY
(Tables 1-3)

Various body parts were measured on 40 *L. putnami* (3.1-7.6 mm) and 64 *P. americanus* (2.4-7.3 mm) larvae to examine developmental morphology. Body proportions are summarized and compared in Table 3.

The most important morphological character for separating *L. putnami* from *P. americanus*, particularly during the yolk-sac and preflexion

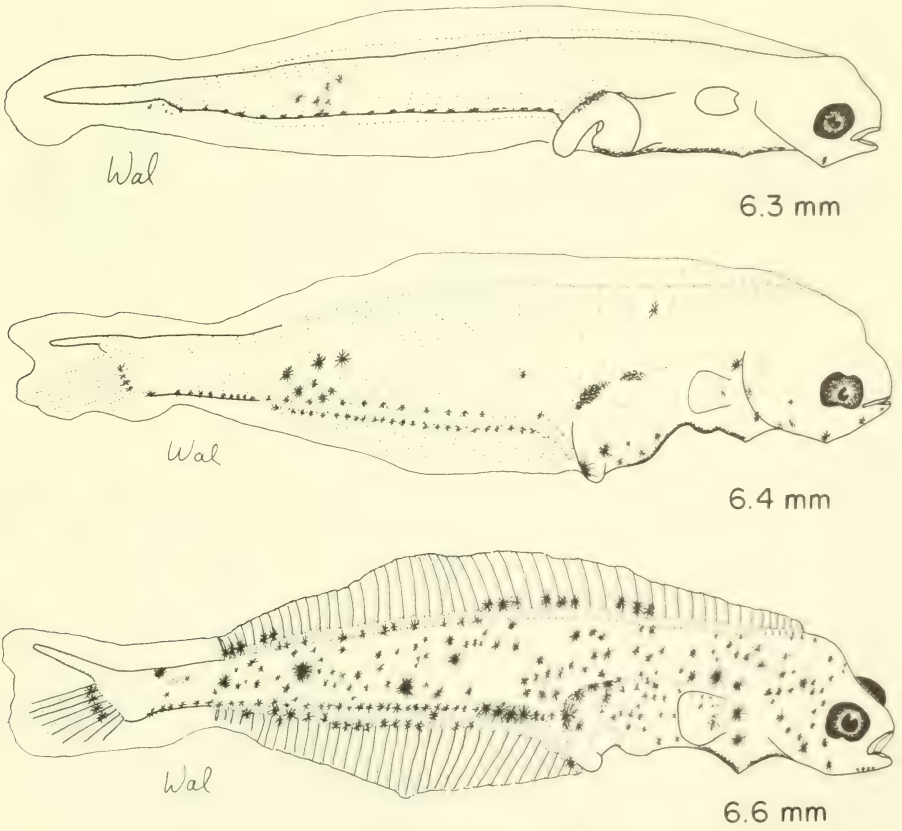


FIGURE 3.—Flexion larvae of *Liopsetta putnami*.

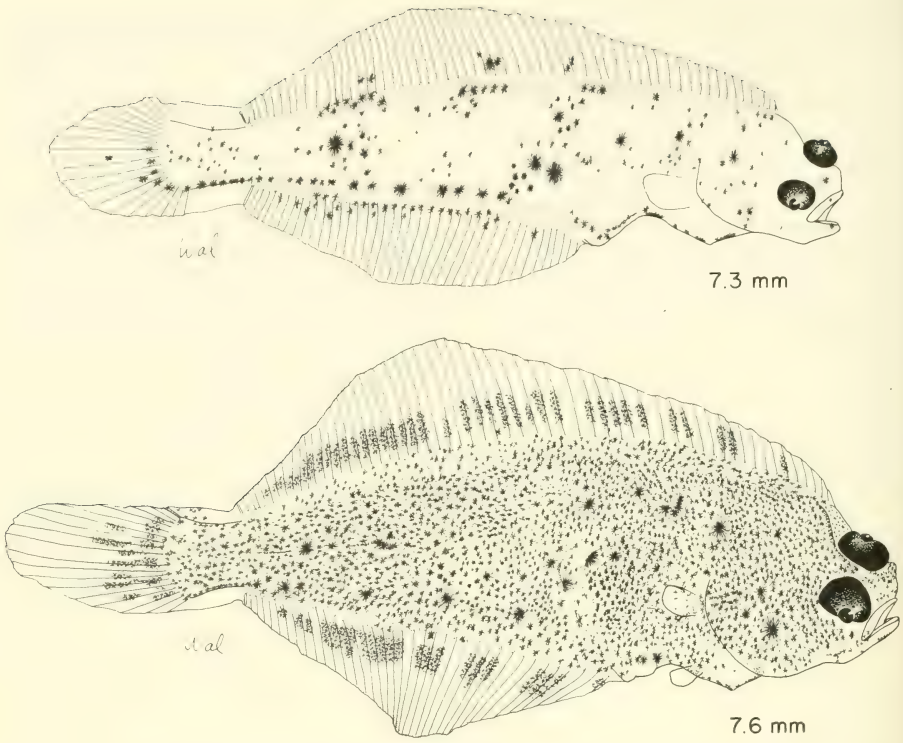


FIGURE 4.—Postflexion and transforming larvae (7.1 and 7.6 mm) of *Liopsetta putnami*.

stages, is snout to anus length/standard length. In *L. putnami* it averages 43.6 and 41.2% for yolk-sac and preflexion larvae while in *P. americanus* it averages 33.3 and 37.6% for yolk-sac and preflexion larvae.

FIN DEVELOPMENT

Newly hatched larvae of both *L. putnami* and *P. americanus* have an undifferentiated fin fold extending along the body midline from the head around the notochord tip to the anus. No other fins were observed on the smallest *L. putnami* larva (3.1 mm); however, the smallest *P. americanus* larva (2.4 mm) and a 3.8 mm *L. putnami* larva had undifferentiated pectoral fin folds.

Pectoral fin rays are the first to begin development in both *L. putnami* and *P. americanus*, by 5.2 and 5.3 mm. However, pectoral fin rays are the last to complete development, completed between 8.5 and 13 mm in *L. putnami* (Laszlo 1972) and by 13 mm in *P. americanus*. Pectoral fin length is greatest in both species during the preflexion and flexion periods, averaging 7.8 and 7.1% SL in *L. putnami* and 7.7 and 7.8% SL in *P. americanus*, and shortest during yolk-sac and postflexion stages, averaging 3.8 and 5.0% SL in *L. putnami* and 3.0 and 4.7% SL in *P. americanus*. Dorsal, anal, and caudal fin rays begin development in preflexion *L. putnami* and *P. americanus* at ≈5.9 and ≈5.6 mm. Adult complements of dorsal and anal fin rays and principal caudal fin rays are present by ≈8 and ≈7 mm. Fin rays within dorsal and anal fins of both species seem to form simultaneously except the two or three posteriormost rays in each fin which form last. Principal caudal fin rays form first and

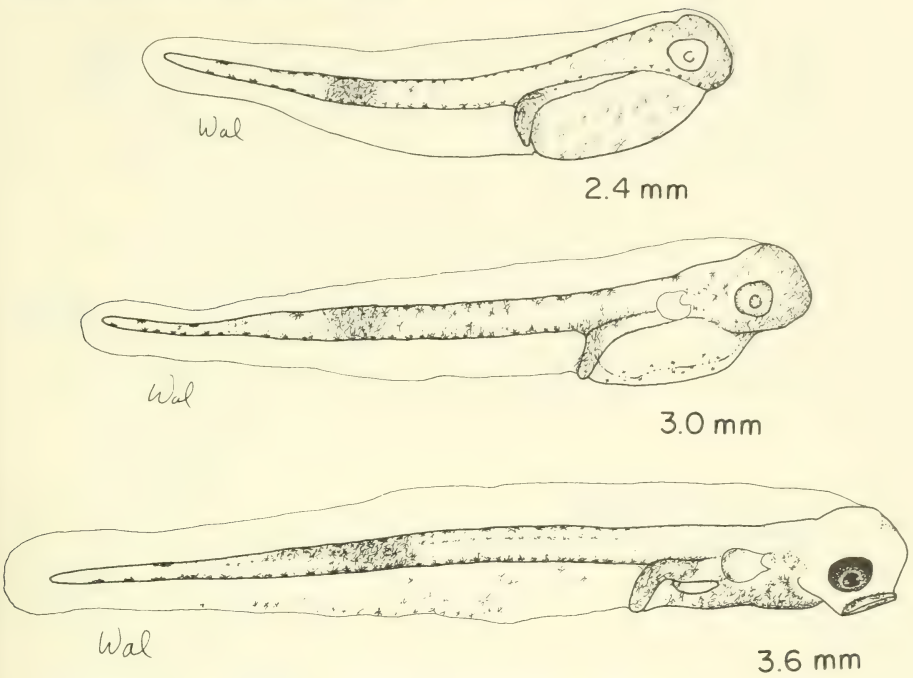


FIGURE 5.—Yolk-sac larvae of *Pseudopleuronectes americanus*.

secondary rays are gradually added anteriorly. The pelvic fin bud appears at ≈7 mm in postflexion *L. putnami* larvae. Fin rays begin to develop by 7.6 mm, and development is completed by 13 mm (Laszlo 1972). The pelvic fin bud appears at ≈6.6 mm in postflexion *P. americanus* larvae; and development is complete by 7.3 mm.

PIGMENTATION

Liopsetta putnami

The eyes of *L. putnami* are darkly pigmented at hatching. Small external melanophores are scattered over the head of the smallest larva (3.1 mm). These melanophores appear to migrate ventrolaterally, appearing on the ventral surface of the head between the isthmus and the cleithrum by ≈4.7 mm, and are aligned here on all specimens >5.4 mm long. This row often appears as a solid line of pigment due to the expanded condition of individual melanophores. A melanophore appears at the angle of the lower jaw between 4.8 and 5.4 mm, and one or two melanophores are present at this location on all specimens >5.4 mm. One or two melanophores are present at the tip of the lower jaw on most specimens >5.8 mm. A large stellate melanophore appears below the lateral midline of the head, anterior to the cleithrum at 5.2 mm. Larvae >5.4 mm often have 4-6 melanophores, internal and external, in this area. A few external melanophores appear scattered over the head, on and under the operculum, by 7.3 mm. Flexion and postflexion larvae >6.6 mm rapidly acquire the dense scattering of external melanophores characteristic of juveniles.

In the abdominal region small external melanophores scattered over the dorsolateral surfaces of the hindgut are present on the smallest larva (3.1 mm). An internal patch over the hindgut is present on all specimens in the series. The small external melanophores migrate ventrolaterally

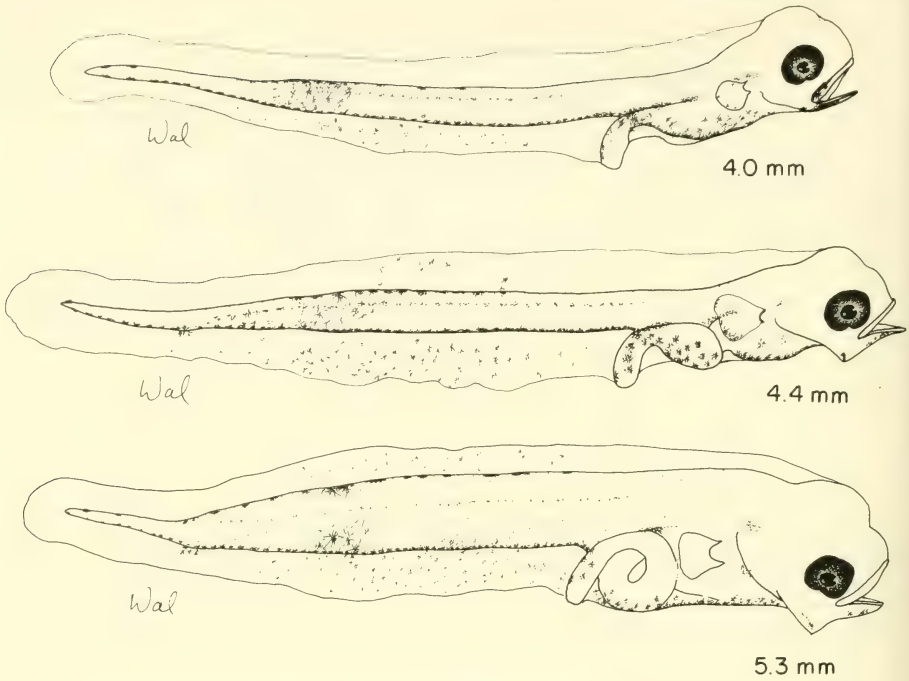


FIGURE 6.—Preflexion larvae (4.0 and 4.4 mm) and flexion larva (5.3 mm) of *Pseudopleuronectes americanus*.

becoming scattered on only the ventral surface of the body and yolk sac by 4.8 mm and form a row along the ventral midline on all specimens larger than ≈5.2 mm. This row extends from the cleithrum, where it is continuous with the row on the ventral midline of the head, to the center of the abdominal region where it becomes indistinct, merging with a group of melanophores scattered on the ventrolateral body surface between 6.6 and 7.0 mm. Specimens >7.0 mm rapidly acquire the dense scattering of external melanophores over the body surface characteristic of juveniles.

Small external melanophores are scattered over the postanal region, and a vertical band of concentrated melanophores of various sizes is present across the center of the postanal region in the smallest larva (3.1 mm). The scattered external melanophores migrate ventrolaterally and are present only on the ventrolateral surfaces by ≈4.6 mm. An irregular row of melanophores extends from the anus to the vertical pigment band along both sides of the ventral midline, and a single irregular row of melanophores along the ventral midline extends posteriorly from the pigment band on specimens 4.3-5.4 mm long. Usually one to several small melanophores appear somewhat separated from the row and located just anterior to the notochord tip. The vertical pigment band is distinct on larvae <5.4 mm, but it is usually represented by only a few large stellate melanophores on larger larvae. These melanophores become indistinguishable from other external melanophores which become scattered over the body on large larvae, >6.6 mm, indicating the initial development of the juvenile pigment pattern.

The fin folds of the smallest *L. putnami* larva are not pigmented. At ≈5.2 mm one or two melanophores move from the body onto the fin membrane just anteroventral to the notochord tip.

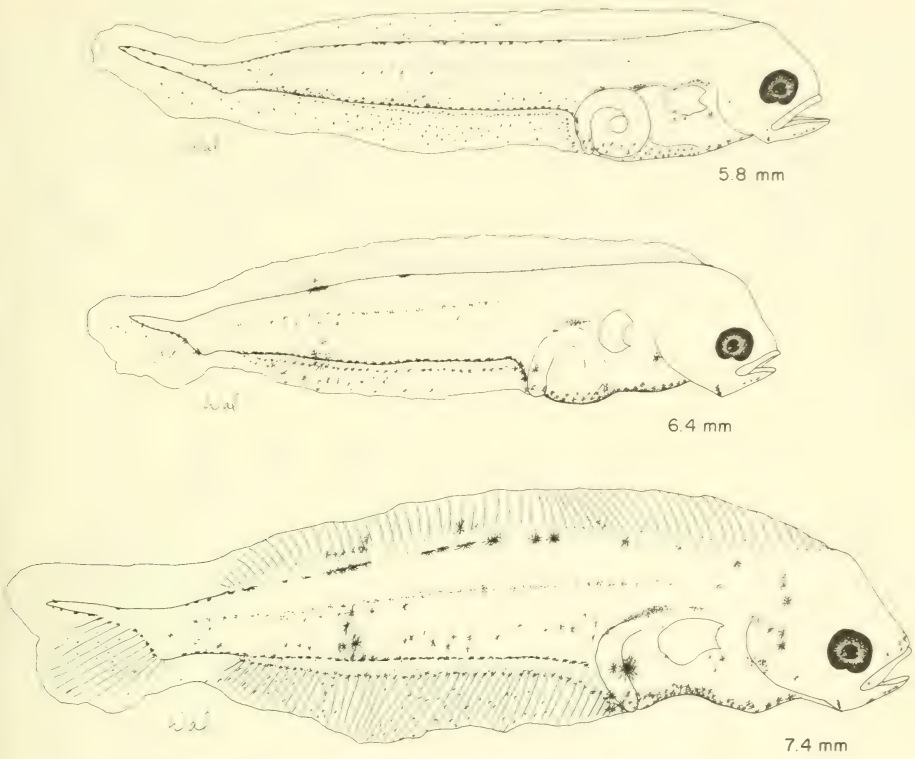


FIGURE 7.—Flexion larvae of *Pseudopleuronectes americanus*.

Several additional melanophores appear at this location by 6.3 mm and appear on the caudal fin near the base of the caudal fin rays after they form. As the pterygiophores associated with the anal fin rays begin to develop, between 6.3 and 6.4 mm, melanophores separate from the postanal ventral midline rows and appear as an irregular row along the distal margins of the pterygiophores and along the bases of the dorsal and anal rays by 6.6 mm. A broken band of melanophores develops in the proximal one-third of the dorsal and anal fins by 7.6 mm.

Scattered metallic yellow chromatophores were present over the head and body of newly hatched larvae. These chromatophores disappear soon after preservation in Formalin. No additional observations of chromatophore patterns were possible on larger field-collected larvae.

Pseudopleuronectes americanus

The eyes of *P. americanus* lack pigmentation at hatching (≈2.4 mm). Pigmentation begins to appear in the eyes of *P. americanus* at ≈2.9 mm, and the eyes are completely pigmented by 3.5 mm. Expanded external melanophores are scattered over the head of the smallest larva (2.4 mm). These melanophores are faint and may be difficult to see. Melanophores over the dorsolateral surfaces of the head disappear by ≈3.5 mm. A few melanophores remain on the upper and lower jaws and along the ventral midline of the head (gular and isthmus regions). No evidence of melanophore migration was observed in *P. americanus*. One to several internal melanophores are present along the anterior edge of the cleithrum often appearing under the operculum on larvae >2.6 mm. One or two

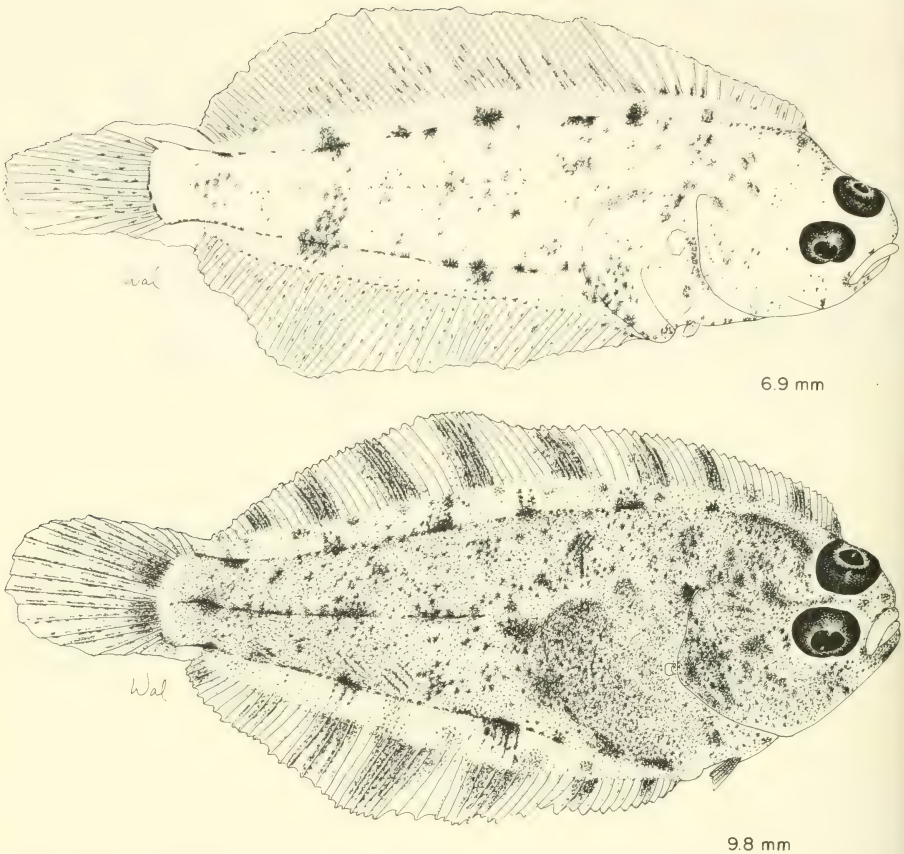


FIGURE 8.—Flexion, transforming, larva (6.9 mm) and postflexion, transforming, larva (9.8 mm) of *Pseudopleuronectes americanus*.

melanophores are present at the articulation of the lower jaw on larvae >3.4 mm. A few external melanophores appear on the snout and operculum of preflexion larvae >6.6 mm. Postflexion larvae (>5.8 mm) rapidly acquire a covering of external melanophores, characteristic of juveniles, as transformation proceeds.

External melanophores are scattered over the abdominal region of the smallest larva (2.4 mm) with greatest concentrations along the dorsal surface of the body and on the ventrolateral surface of the yolk sac. Internal melanophores are present in a patch over the posterior hindgut near the anus and over the middle of the gut. By 3.6 mm pigmentation disappears from the dorsolateral surface of the abdominal region, and the melanophores which had been scattered over the yolk sac are on the ventrolateral surfaces of the body. Some of these form a row which is often expanded and appears as a solid line between the anus and the cleithrum with some on the ventrolateral surface on each side of the line. Also, by 3.6 mm, one to several internal melanophores appear in the vicinity of the pectoral fin base posterior to the cleithrum. By 4.4 mm, internal melanophores are present over the notochord in this region. No further pigmentation changes occur until external melanophores begin to appear scattered over

TABLE 1.—Measurements (millimeters) of larval *Liopsetta putnami*. Specimens above dashed line are yolk-sac larvae.

Standard length	Total length	Body depth at pectoral fin base	Body depth at anus	Maximum body depth at pectoral fin base	Maximum body depth at anus	Snout to anus length	Head length	Eye diameter	Upper jaw length	Snout length	Pectoral fin length
3.1	3.2	0.40	0.36	—	—	1.5	0.44	0.18	—	—	—
3.6	3.8	0.40	0.36	—	—	1.8	0.50	0.24	—	0.16	0.18
4.0	4.1	0.34	0.22	—	—	1.6	0.52	0.24	—	0.14	0.14
4.3	4.4	0.36	0.24	—	—	2.0	0.56	0.24	—	0.16	—
4.4	4.5	0.38	0.26	—	—	1.8	0.60	0.26	—	0.22	0.10
4.6	4.8	0.40	0.24	—	—	1.8	0.60	0.24	—	0.16	0.18
4.8	5.0	0.50	0.28	—	—	1.9	0.62	0.26	0.14	0.14	0.34
4.8	5.0	0.54	0.28	—	—	—	0.64	0.26	—	0.12	0.14
4.8	5.0	0.46	0.26	—	—	2.1	0.62	0.24	0.14	0.18	0.16
4.9	5.2	0.40	0.26	—	—	2.2	0.64	0.26	—	0.16	0.18
4.9	5.1	0.40	0.26	—	—	2.1	0.60	0.26	—	0.16	0.12
5.0	5.1	0.38	0.30	—	—	2.2	0.68	0.26	—	0.20	0.18
[1]5.2	5.3	0.46	0.32	—	—	2.2	0.74	0.26	0.20	0.18	0.30
[1]5.2	5.3	0.54	0.34	—	—	2.4	0.80	0.28	0.18	0.16	0.32
[1]5.4	5.7	0.62	0.40	—	—	2.4	0.80	0.29	0.16	0.12	0.38
[1]5.4	5.7	0.66	0.42	—	—	2.1	0.80	0.26	0.20	0.14	0.36
[1]5.5	5.8	0.82	0.62	—	—	2.1	0.96	0.30	0.18	0.10	0.52
[1]5.5	5.7	0.76	0.60	—	—	2.4	1.0	0.29	0.30	0.16	0.56
[1]5.7	5.9	0.74	0.60	—	—	2.4	1.1	0.28	0.26	0.12	0.52
[1]5.8	6.0	0.78	0.62	—	—	2.3	1.0	0.30	0.38	0.20	0.52
[1]5.9	6.2	0.74	0.44	—	—	2.4	0.96	0.27	0.28	0.16	0.44
[2]5.9	6.2	0.80	0.70	—	—	2.6	1.2	0.30	0.32	0.20	0.40
[1]5.9	6.2	0.78	0.56	—	—	2.3	1.1	0.30	0.36	0.18	0.40
[2]6.2	6.3	0.98	0.90	1.0	0.94	2.5	1.1	0.32	0.42	0.26	0.54
[1]6.3	6.6	0.78	0.56	—	—	2.5	1.0	0.30	0.32	0.16	0.48
[1]6.4	6.6	1.0	0.92	1.1	0.94	2.7	1.2	0.32	0.46	0.24	0.50
[1]6.5	6.7	0.74	0.52	—	—	2.7	1.1	0.32	0.30	0.16	0.46
[1]6.6	6.8	0.78	0.60	—	—	2.5	1.0	0.31	0.30	0.14	0.54
[2]6.6	6.9	1.0	0.80	1.1	0.86	2.7	1.2	0.33	0.40	0.20	0.46
[2]6.6	6.8	1.1	1.1	1.2	1.1	2.8	1.4	0.34	0.42	0.22	0.54
[2]6.7	6.9	0.92	0.80	0.96	0.86	2.7	1.0	0.32	0.40	0.20	0.44
[2]6.8	7.1	0.84	0.72	0.89	0.74	2.8	1.2	0.32	0.32	0.18	0.40
[2]6.9	7.1	0.92	0.76	0.96	0.80	2.6	1.2	0.34	0.40	0.20	0.50
[2]7.0	7.4	1.1	1.1	1.2	1.1	2.8	1.3	0.34	0.40	0.16	0.52
[2]7.0	7.3	1.2	1.1	1.2	1.2	2.8	1.4	0.32	0.40	0.20	0.50
[2]7.0	7.4	1.1	1.0	1.1	1.1	2.8	1.3	0.32	0.40	0.18	0.50
[3]7.1	8.1	1.5	1.4	1.6	1.5	2.6	1.5	0.36	0.44	0.26	0.60
[2]7.3	7.6	1.1	1.0	1.2	1.1	3.0	1.3	0.36	0.40	0.18	0.50
[2]7.3	7.5	1.1	1.0	1.2	1.1	2.8	1.3	0.34	0.40	0.20	0.48
[3]7.6	9.3	—	—	2.4	2.4	2.7	2.1	0.54	0.56	0.28	0.24

[1] = preflexion larvae; [2] = flexion larvae; [3] = postflexion larvae.

the abdominal region of preflexion larvae, >6.2 mm, as metamorphosis begins and the juvenile pattern of dense melanophore covering begins to develop.

A vertical band of concentrated melanophores of various sizes is present across the center of the postanal region in the smallest larva (2.4 mm). External melanophores are aligned in irregular rows on both sides of the ventral midline between the anus and the postanal band. A single irregular row of melanophores extends along the ventral surface from the vertical band nearly to the notochord tip. An irregular row is also present along the dorsal midline extending posteriorly nearly to the notochord tip. Only a few scattered melanophores appear laterally. A row of internal melanophores over the notochord is present on all larvae longer than ≈3.2 mm. The postanal band becomes less distinct, usually represented by only a few large stellate melanophores, in larvae >5.0 mm. Scattered external melanophores begin to appear over the lateral surfaces of preflexion larvae >5.6 mm and continue to increase in number through the larval period. Concentrated pigment spots develop along the dorsal and ventral body surfaces in transforming larvae >5.8 mm.

The fin folds of the smallest *P. americanus* larva are not pigmented. Various authors (Sullivan 1915; Breder 1924; Bigelow and Schroeder 1953; Lippson and Moran 1974) have illustrated small larvae with melanophores extending onto the dorsal and anal fin folds (probably no melanophores were centered on the fin folds) from the vertical postanal band. Their illustrations were of artificially reared larvae. I observed no melanophores extending onto the dorsal and anal fin folds of field-collected larvae; however, reared larvae commonly have somewhat increased pigment due mostly to light conditions which can be altered to change the size of melanophores (Milos and Dingle 1978). A few small melanophores appear along the margin of the pectoral fin fold at 3.5 mm and disappear

TABLE 2.—Measurements (millimeters) of larval *Pseudopleuronectes americanus*. Specimens above dashed line are yolk-sac larvae.

Standard length	Total length	Body depth at pectoral fin base	Body depth at anus	Maximum body depth at pectoral fin base	Maximum body depth at anus	Snout to anus length	Head length	Eye diameter	Upper jaw length	Snout length	Pectoral fin length
2.4	2.5	0.20	0.14	—	—	0.92	0.39	0.17	—	0.08	0.05
2.6	2.7	0.18	0.15	—	—	0.92	0.38	0.16	—	0.10	0.04
2.6	2.6	0.24	0.14	—	—	0.85	0.39	0.17	—	0.11	0.04
2.7	2.7	0.24	0.15	—	—	0.94	0.42	0.17	—	0.10	0.04
2.8	2.8	0.25	0.14	—	—	0.90	0.39	0.17	—	0.10	0.08
2.8	2.9	0.24	0.14	—	—	0.98	0.39	0.18	—	0.10	0.05
2.8	3.0	0.24	0.15	—	—	1.0	0.42	0.18	0.16	0.12	—
2.9	3.0	0.19	0.13	—	—	0.96	0.39	0.17	0.14	0.12	0.06
2.9	3.0	0.21	0.14	—	—	0.90	0.40	0.18	—	0.12	0.04
2.9	3.0	0.24	0.15	—	—	0.96	0.42	0.18	0.16	0.14	0.06
3.0	3.2	0.24	0.15	—	—	1.0	0.42	0.18	0.18	0.14	0.05
3.3	3.4	0.25	0.14	—	—	1.0	0.42	0.18	0.18	0.10	0.06
3.3	3.5	0.34	0.15	—	—	1.0	0.42	0.18	0.18	0.08	0.10
3.4	3.6	0.36	0.14	—	—	1.1	0.42	0.20	0.18	0.08	0.10
3.4	3.6	0.38	0.15	—	—	1.2	0.48	0.20	0.19	0.10	0.20
3.5	3.7	0.33	0.14	—	—	1.1	0.44	0.18	0.17	0.09	0.20
3.5	3.7	0.34	0.15	—	—	1.2	0.46	0.20	0.20	0.09	0.20
3.5	3.7	0.34	0.15	—	—	1.1	0.45	0.18	0.19	0.10	0.19
3.6	3.8	0.33	0.14	—	—	1.2	0.47	0.20	0.21	0.13	0.20
[1]3.7	3.9	0.48	0.24	—	—	1.4	0.66	0.24	0.26	0.12	0.30
[1]4.0	4.3	0.42	0.19	—	—	1.5	0.62	—	0.26	—	0.26
[1]4.2	4.3	0.60	0.30	—	—	1.5	0.76	0.27	0.26	0.18	0.32
[1]4.4	4.5	0.50	0.22	—	—	1.6	0.70	0.26	0.22	0.14	0.32
[1]4.4	4.5	0.50	0.22	—	—	1.5	0.68	0.24	0.22	0.15	0.30
[1]4.5	4.6	0.66	0.32	—	—	1.6	0.80	0.28	0.24	0.12	—
[1]4.5	4.6	0.70	0.35	—	—	1.7	0.82	0.27	0.26	0.18	0.30
[1]4.6	4.7	0.74	0.38	—	—	1.8	0.92	0.32	0.38	0.20	0.28
[2]4.8	4.9	0.80	0.46	—	—	1.8	0.88	0.31	0.30	0.18	0.30
[1]4.9	5.2	0.78	0.44	—	—	1.8	0.98	—	—	—	0.40
[1]4.9	5.2	—	—	—	—	2.0	1.1	0.34	0.32	0.20	0.45
[1]5.1	5.3	0.85	0.54	—	—	2.0	1.0	0.33	0.32	0.14	0.44
[1]5.2	5.4	0.96	0.64	—	—	2.0	1.0	0.34	0.38	0.24	0.44
[2]5.3	5.5	0.94	0.56	—	—	2.1	0.98	0.33	0.34	0.22	0.44
[1]5.4	5.5	0.90	0.60	—	—	2.1	1.1	0.33	0.35	0.18	—
[2]5.6	5.7	1.1	0.82	—	—	2.3	1.2	0.34	0.40	0.24	0.48
[1]5.7	5.8	1.1	0.78	—	—	2.1	1.2	0.34	0.40	0.22	0.45
[1]5.7	5.8	1.1	0.72	—	—	2.2	1.1	0.34	0.40	0.26	0.46
[2]5.8	6.1	1.1	0.70	—	—	2.3	1.2	0.36	0.36	0.20	0.52
[2]6.0	6.2	1.1	0.80	—	—	2.3	1.3	0.36	0.36	0.20	0.48
[2]6.2	6.3	1.3	0.88	—	1.0	2.4	1.3	0.36	0.42	0.26	0.55
[2]6.3	6.4	1.3	0.98	1.4	1.2	2.4	1.4	0.40	0.48	0.26	0.54
[2]6.3	6.4	1.3	0.88	—	1.1	2.4	1.4	0.36	0.44	0.28	0.50
[2]6.4	6.5	1.2	0.86	1.3	1.1	2.4	1.3	0.34	0.40	0.20	0.48
[2]6.5	6.7	1.2	0.84	1.3	1.0	2.6	1.4	0.38	0.42	0.26	0.42
[3]6.6	6.7	1.3	0.96	1.4	1.2	2.5	1.4	0.38	0.42	0.22	0.52
[3]6.6	6.8	1.4	1.1	1.6	1.5	2.4	1.6	0.39	0.48	0.28	0.58
[2]6.8	6.9	1.3	1.0	1.4	1.3	2.5	1.5	0.38	0.40	0.26	0.50
[2]6.9	7.2	1.3	0.96	1.4	1.2	2.6	1.5	0.40	0.46	0.27	0.52
[2]7.0	7.3	1.4	1.1	1.5	1.2	2.7	1.5	0.41	0.44	0.28	0.64
[2]7.1	7.3	1.3	0.94	1.4	1.2	2.6	1.3	0.39	0.44	0.24	0.58
[2]7.3	7.8	1.7	1.4	1.8	1.7	2.6	1.8	0.46	0.44	0.32	0.54
[2]7.4	7.7	1.4	1.1	1.5	1.2	2.4	1.5	0.38	0.44	0.26	0.50
[3]5.7	—	1.7	1.2	1.8	1.6	2.0	1.6	0.48	0.49	0.22	—
[3]6.0	—	1.7	1.3	1.7	1.7	2.4	1.7	0.46	0.48	0.34	0.40
[3]6.2	—	1.9	1.3	2.2	1.8	2.3	1.7	0.46	0.46	0.38	0.34
[3]6.4	—	2.2	1.5	2.4	2.1	2.3	1.7	0.54	0.51	0.34	0.10
[3]6.6	7.7	1.6	1.3	1.8	1.7	2.4	1.8	0.46	0.44	0.38	0.42
[3]6.6	—	1.7	1.4	1.8	1.9	2.5	1.8	0.48	0.44	0.34	0.41
[3]6.9	8.2	1.9	1.5	2.1	2.1	2.3	1.8	0.50	0.46	0.40	0.30
[3]7.0	8.4	1.9	1.5	2.0	2.1	2.4	1.8	0.46	0.42	0.36	0.30
[2]7.0	8.4	2.2	1.7	2.4	2.4	2.2	2.0	0.58	0.56	0.44	0.10
[3]7.1	8.5	2.0	1.5	2.1	1.8	2.4	1.9	0.51	0.40	0.40	0.20
[3]7.3	7.9	2.5	1.8	2.8	2.2	2.4	2.0	0.62	0.38	0.38	—

[1] = preflexion larvae; [2] = flexion larvae; [3] = postflexion larvae.

again in flexion larvae by ≈6.4 mm. Scattered melanophores appear on the anal fin fold at 3.6 mm, and a few appear at the center of the dorsal fin fold at ≈4.2 mm. These melanophores remain through the larval period with pigment bars, characteristic of juveniles, developing on the dorsal and anal fins in flexion and postflexion larvae >7.3 mm. By 4.4 mm a few melanophores appear on the fin fold at about the notochord flexion point. These melanophores increase in number with development and are visible on the caudal fin during and after development of the caudal fin rays.

TABLE 3.—Body proportions of larval *Liopsetta putnami* and *Pseudopleuronectes americanus*. Values given are percentage of standard length (SL) or head length (HL) including mean, standard deviation, and range in parentheses. Number of specimens measured may be derived from Tables 1 and 2.

Item	*Liopsetta putnami*	*Pseudopleuronectes americanus*
Body depth at pectoral fin base/SL		
Yolk sac	9.4± 1.61(7.6-12.9)	8.8±1.23(6.6-11.2)
Preflexion	12.5± 1.74(8.8-13.8)	15.2±2.87(10.5-19.3)
Flexion	15.4± 2.14(12.4-20.5)	19.3±1.49(16.7-23.3)
Postflexion	23.6±11.38(15.5-31.6)	28.6±3.85(21.2-34.2)
Body depth at anus/SL:		
Yolk sac	6.4± 2.08(5.2-11.6)	4.8±0.61(3.9-5.9)
Preflexion	9.2± 2.22(6.2-14.4)	8.6±2.99(4.8-13.7)
Flexion	13.5± 1.99(11.0-16.7)	13.9±2.11(9.6-19.2)
Postflexion	25.6± 8.41(19.7-31.6)	21.3±1.83(16.7-24.3)
Maximum body depth at pectoral fin base/SL:		
Yolk sac	9.4± 1.61(7.6-12.9)	8.8±1.23(6.6-11.2)
Preflexion	12.6± 1.89(8.8-16.6)	15.2±2.87(10.5-19.3)
Flexion	15.6± 1.52(13.1-17.6)	20.2±1.80(16.7-24.7)
Postflexion	28.1± 7.50(22.8-33.4)	31.1±4.45(24.2-38.4)
Maximum body depth at anus/SL:		
Yolk sac	6.4± 2.08(5.2-11.6)	4.8±6.09(3.9-5.9)
Preflexion	9.2± 2.28(6.2-14.7)	8.6±2.99(4.8-13.7)
Flexion	14.1± 2.00(10.9-17.0)	16.1±3.35(10.6-23.3)
Postflexion	26.8± 7.67(21.4-32.1)	28.8±3.17(22.7-34.3)
Snout to anus length/SL:		
Yolk sac	43.6± 3.62(39.1-50.0)	33.3±2.03(30.3-37.7)
Preflexion	41.2± 2.46(37.9-46.2)	37.6±1.72(34.1-40.8)
Flexion	40.5± 1.67(36.6-44.1)	37.9±1.95(32.4-41.1)
Postflexion	36.0± 0.78(35.5-36.6)	35.4±2.39(24.2-28.6)
Head length/SL:		
Yolk sac	13.2± 0.53(12.2-14.2)	13.9±1.05(12.4-16.0)
Preflexion	15.4± 4.31(14.2-18.8)	18.7±2.03(15.5-22.4)
Flexion	18.3± 1.63(14.9-21.2)	21.0±1.61(18.3-24.7)
Postflexion	24.4± 4.60(21.1-27.6)	27.0±1.22(24.2-28.6)
Eye diameter/HL:		
Yolk sac	41.9± 2.87(38.2-48.0)	43.1±1.81(40.0-47.6)
Preflexion	31.2± 3.57(25.5-37.5)	33.4±2.55(31.1-37.1)
Flexion	26.8± 2.28(24.3-32.0)	28.3±2.71(25.0-33.7)
Postflexion	24.8± 1.20(24.0-25.7)	27.1±2.36(24.0-31.4)
Upper jaw length/HL:		
Yolk sac	22.6± 0.00(22.6)	41.0±2.80(35.9-44.7)
Preflexion	28.2± 5.96(18.8-38.3)	34.5±4.18(30.0-41.9)
Flexion	31.5± 3.57(26.7-40.0)	31.3±2.47(26.7-34.7)
Postflexion	28.0± 1.84(26.7-29.3)	26.0±3.67(19.0-30.6)
Snout length/HL:		
Yolk sac	27.5± 4.69(18.8-36.7)	25.2±4.71(19.0-33.3)
Preflexion	16.6± 3.72(10.4-24.3)	19.8±3.37(14.0-24.0)
Flexion	16.2± 3.05(12.3-20.0)	18.3±1.92(15.4-22.4)
Postflexion	15.3± 2.83(13.3-17.3)	19.8±2.40(13.8-22.4)
Pectoral fin length/SL:		
Yolk sac	3.8± 1.38(2.4-7.1)	3.0±1.75(1.4-5.9)
Preflexion	7.8± 1.30(5.8-10.2)	7.7±0.92(6.1-9.2)
Flexion	7.1± 0.74(5.9-8.5)	7.8±0.85(6.2-9.1)
Postflexion	5.0± 2.55(3.2-6.8)	4.7±2.48(0.8-8.8)

Melanophore numbers on the caudal fin membrane increase through flexion and postflexion periods with the entire fin becoming covered with melanophores, including an intense pigment patch near the fin base, by 9.8 mm.

ACKNOWLEDGMENTS

Special thanks are extended to H. H. DeWitt for allowing me to use his larval fish collections and radiographs of juvenile specimens. Additional specimens were provided by S. M. Fried, J. L. Laroche, B. P. Lindsey, and J. D. McCleave. Gilbert Jaeger helped with the field collecting. H. H. DeWitt, J. D. McCleave, S. L. Richardson, and W. G. Smith read the manuscript and provided useful comments.

LITERATURE CITED

BIGELOW, H. B., AND W. C. SCHROEDER.
1953. Fishes of the Gulf of Maine. U.S. Fish Wildl. Serv. Fish. Bull. 53, 577 p.

BIGELOW, H. B., AND W. W. WELSH.
1925. Fishes of the Gulf of Maine. Bull. U.S. Bur. Fish. 40(1), 567 p.

BREDER, C. M., JR.
1924. Some embryonic and larval stages of the winter flounder. Bull. U.S. Bur. Fish. 38:311-315.

JORDAN, D. S., AND B. W. EVERMANN.
1898. The fishes of North and Middle America: A descriptive catalogue of the species of fish-like vertebrates found in the waters of North America, north of the Isthmus of Panama. Part II. Bull. U.S. Mus. 47:1241-2183.

KLEIN-MACPHEE, G.
1978. Synopsis of biological data for the winter flounder, *Pseudopleuronectes americanus* (Walbaum). U.S. Dep. Commer., NOAA Tech. Rep. NMFS Circ. 414, 43 p.

LEIM, A. H., AND W. B. SCOTT.
1966. Fishes of the Atlantic coast of Canada. Fish. Res. Board Can., Bull. 155, 485 p.

LIPPSON, A. J., AND R. L. MORAN.
1974. Manual for identification of early developmental stages of fishes of the Potomac River estuary. Martin Marietta Corp., Baltimore, Md., 282 p.

LASZLO, P. T.
1972. Age-growth, food, and reproduction of the smooth flounder *Liopsetta putnami* (Gill) in Great Bay, New Hampshire. Ph. D. Diss., Univ. New Hampshire, 86 p.

MARTIN, F. D., AND G. E. DREWRY.
1978. Development of fishes of the mid-Atlantic Bight: an atlas of egg, larval and juvenile stages. Vol. VI, Stromateidae through Ogcocephalidae. U.S. Fish Wildl. Serv., Off. Biol. Serv., 78/12, 416 p.

MILOS, N., AND A. D. DINGLE.
1978. Dynamics of pigment pattern formation in the zebrafish, *Brachydanio rerio*. I. Establishment and regulation of the lateral line melanophore stripe during the first eight days of development. J. Exp. Zool. 205:205-216.

NORMAN, J. R.
1934. A systematic monograph of the flatfishes (Heterosomata). Vol. I. Psettodidae, Bothidae, Pleuronectidae. Br. Mus. (Nat. Hist.), 459 p.

SCOTTON, L. N., R. E. SMITH, N. S. SMITH, K. S. PRICE, AND D. P. DE SYLVA.
1973. Pictoral guide to the fish larvae of Delaware Bay, with information and bibliographies useful for the study of fish larvae. Del. Bay Rep. Ser. 7, Coll. Mar. Stud., Univ. Del., 206 p.

SULLIVAN, W. E.
1915. A description of the young stages of the winter flounder. Trans. Am. Fish. Soc. 44:125-136.

SEASONALITY OF FISHES OCCUPYING A SURF ZONE HABITAT IN THE NORTHERN GULF OF MEXICO

TIMOTHY MODDE[1] AND STEPHEN T. ROSS[2]

ABSTRACT

The ichthyofauna occupying the surf zone habitat of Horn Island, Mississippi, between 1975 and 1977 was dominated by immature clupeiform fishes. The dusky anchovy, *Anchoa lyolepis*, and the scaled sardine, *Harengula jaguana*, together constituted 80.2% of the 154,469 fishes collected. The greatest number of fishes were collected in the late spring and summer, followed by a secondary peak in late winter. Occurrence of the fishes within the surf zone is divided into three categories according to seasonal utilization: spring and summer, summer only, and winter. Factors affecting numerical abundance within the surf zone differed among the most frequently appearing species. Differences in the numbers of clupeiform fishes—*A. lyolepis*; *A. hepsetus*, striped anchovy; and *H. jaguana*—were more closely associated with diel changes including tidal stage and time of day. The abundance of the Florida pompano, *Trachinotus carolinus*, and the gulf kingfish, *Menticirrhus littoralis*, were more dependent upon seasonal effects such as temperature.

Relatively few studies have investigated the role of exposed surf zone habitats in the early life history of fishes. While Springer and Woodburn (1960) described the surf zone region as an "extreme habitat offering little environmental diversity," this habitat does provide several benefits to fishes. Advantages suggested by Warfel and Merriman (1944) included the abundance of food (concentrated by incoming tides), increased metabolic efficiency via heat acquisition, and protection from predation.

Surf zone ichthyofaunas are numerically dominated by relatively few species. For instance, McFarland (1963) stated that 60-80% of the ichthyofauna occupying the surf regions along the south Atlantic and Texas coasts was comprised of only a few species. Gunter (1958) found high similarity in species composition between Mustang Island, Texas, and Atlantic coast surf zones and suggested that the surf zone region was dominated by a small group of species which remained relatively constant over wide geographical areas.

Much of the literature regarding shore zone fishes is restricted to either descriptions of species occurrence or seasonal characterizations, seldom exceeding one annual cycle. Reid (1955a, b), Schaefer (1967), and Hillman et al. (1977) have sampled the same habitats in successive seasons and have observed annual changes in species composition. Fewer studies have attempted to relate physical or biological parameters to the abundance of fishes within the shallow beach habitat. Gunter (1945) and Warfel and Merriman (1944) attributed the distinct seasonal fluctuations in fish abundance to temperature. Both Anderson et al. (1977) and de Sylva,[3] using multiple regression analyses and crosstabulation, respectively, also indicated that temperature was a significant factor in determining seasonal abundance of the most numerous fish species.

The present study describes seasonal and annual variations in fish species composition and the factors affecting fish occurrences within the surf zone of Horn Island, Miss., a barrier island in the northern Gulf of Mexico.

METHODS

The study area was located along the southern shore of Horn Island, Jackson County, Miss. Horn Island is in a chain of barrier islands lying parallel to the Mississippi-Alabama Gulf coast (Figure 1). The island lies approximately 14 km off the mainland and has a length of 19 km with a maximum width of 1.2 km. The beach is partially protected from oceanic wind-driven waves by a series of sand

[1]Department of Biology, University of Southern Mississippi, SS Box 5018, Hattiesburg, Miss.; present address: Department of Wildlife and Fisheries Sciences, South Dakota State University, Brookings, SD 57007.

[2]Department of Biology, University of Southern Mississippi, SS Box 5018, Hattiesburg, MS 39401.

[3]de Sylva, D. P. 1962. Fishes and ecological conditions in the surf zone of the Delaware River estuary, with notes on other species collected in deeper water. Univ. Del. Mar. Lab Inf. Serv. 5, 164 p.

Manuscript accepted April 1980.
FISHERY BULLETIN: VOL. 78, NO. 4, 1981.

FIGURE 1.—Map of Horn Island, Jackson County, Miss., showing the four sampling areas. The southern side of the island represented the windward shore.

bars which extend the length of the island. The surf zone habitat is characterized by a sand substrate, the absence of any rooted vegetation, and sufficient wave activity to be categorized as a high energy beach (Odum and Copeland 1974).

We began sampling in April 1975 along the southwestern edge of the island (Station 1), and collections were made at about 7-wk intervals until November 1975. From May 1976 to November 1977 we sampled four stations along the windward shore of Horn Island (Figure 1) at about 5-wk intervals (Table 1). We also sampled sheltered beach areas adjacent to Stations 3 and 4 during the summer of 1976. All of the above collections were taken between 0900 and 1600 h c.s.t. (central standard time).

TABLE 1.—Sampling dates for fish taken from the surf zone habitat on the southern shore of Horn Island, Miss., between April 1975 and November 1977. Each collection represents a set of seine hauls at a specific location.

	1975		1976		1977	
Season	Date	No. of collections	Date	No. of collections	Date	No. of collections
Winter			13 Mar.	6	22 Jan.	4
					17 Mar.	5
Spring	12 Apr.	3	23 Apr.	4	28 Apr.	5
	21 June	2	28 May	7	27 May	8
Summer	12 Aug.	3	25 June	11	27 June	5
			23 July	8	23 July	5
			24 Aug.	5	17 Sept.	4
			2 Sept.	8		
Fall	18 Oct.	4	1 Oct.	6	23 Nov.	4
			4 Dec.	5		

Every month between March and September 1976 (excluding August) we sampled either Station 1, 3, or 4 over a 24-h period, taking samples at about 4-h intervals. The choice of station was based in part on the availability of a safe anchorage for our boat. In order to compare data throughout the study, collections made between 1600 and 0900 h were not included in seasonal or annual comparisons.

Fishes were collected with a 3.2 mm Ace[4] mesh bag seine measuring 9.1 × 1.8 m. Hauls were made perpendicular to the beach face beginning 16-18 m offshore. The area sampled extended from the swash zone to the midlongshore trough, and we made an effort to take regular samples only in areas directly exposed to surf. We continued seining at each location until no additional new species were collected; usually 5-9 hauls sufficed. Each collection at each location was thus comprised of a successive number of seine hauls. Fishes collected from all seine hauls at a single station were pooled for analysis. Catch-per-effort data from all stations were pooled to provide monthly means. The study included 613 seine hauls.

Species similarity by months was analyzed by the unpaired group arithmetic average clustering (UPGMA) method (Sneath and Sokal 1973). Only the 15 most abundant species, which were collected in at least 15% of the locations sampled, were analyzed. Pair similarity based on species presence or absence (Odum 1971) was determined by:

$$S = 2C/A + B$$

where C = number of species common to samples a and b,
A = number of species in sample a,
B = number of species in sample b.

We used stepwise multiple regression to define the dominant factors associated with the abundance (fish per seine haul) of the five most frequently occurring species. Environmental parameters selected as independent variables were

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

temperature, salinity, tide level, wave height, beach slope, wind speed, and wind direction. The latter two parameters represented means of the 4-wk period preceding each collection. Wind direction and velocity data were recorded at Keesler Air Force Base on the adjacent mainland. Tide level data were entered as the difference from mean low water and were from tide tables. Because of the absence of data regarding several environmental parameters, collections made during 1975 were not included in the regression analysis.

RESULTS

Annual and Seasonal Occurrence

During the 32-mo study period, 154,469 fishes, representing 14 orders, 42 families, and 76 species, were collected (Table 2). These were primarily late larvae and early juveniles, and only 1.1% exceeded 50 mm SL. The major families represented in the surf zone, in both percent occurrence and numbers collected, were the Engraulidae, Clupeidae,

TABLE 2.—Total number of fishes collected from the surf zone of Horn Island, Miss., between April 1975 and November 1977, and percentage frequency of species occurrence in the collections.

Species	1975	1976	1977	Total	Frequency of occurrence
Carcharhinidae					
Carcharhinus limbatus, blacktip shark		1		1	0.9
Dasyatidae					
Dasyatis sayi, bluntnose stingray		1		1	.9
Megalopidae					
Megalops atlantica, tarpon	2	1		3	2.7
Elopidae					
Elops saurus, ladyfish	2		3	5	2.7
Albulidae					
Albula vulpes, bonefish			4	4	3.6
Ophichthidae					
Myrophis punctatus, speckled worm eel			2	2	1.8
Clupeidae					
Harengula jaguana, scaled sardine	1,941	45,790	12,001	59,732	64.3
Sardinella anchovia, spanish sardine	170	107	27	304	17.0
Opisthonema oglinum, Atlantic thread herring	87	88	1	176	8.9
Brevoortia patronus, gulf menhaden	1,069	1,046	6,733	8,848	17.9
Etrumeus teres, round herring			1	1	.9
Engraulidae					
Anchoa lyolepis, dusky anchovy	6,855	41,690	15,486	64,031	47.3
A. hepsetus, striped anchovy	74	2,656	1,021	3,751	44.6
A. mitchilli, bay anchovy	788	275	1,890	2,953	29.5
A. cubana, cuban anchovy	5	2		7	1.8
Anchoviella perfasciata, flat anchovy	507	514	234	1,255	21.4
Synodontidae					
Synodus foetens, inshore lizard fish	26	30	11	67	18.8
Ariidae					
Arius felis, sea catfish	8	16	6	30	13.4
Gobiesocidae					
Gobiesox strumosus, skilletfish		3	10	13	5.4
Gadidae					
Urophycis regius, spotted hake			1	1	.9
Polynemidae					
Polydactylus octonemus, Atlantic threadfin			2	2	.9
Pomatomidae					
Pomatomus saltatrix, bluefish		11	28	39	8.0
Rachycentridae					
Rachycentron canadum, cobia		4		4	1.8
Sphyraenidae					
Sphyraena borealis, northern sennet		24	106	130	12.5
S. guachancho, guaguanche		7		7	3.6
Scombridae					
Scomberomorus maculatus, spanish mackerel	7	52	4	63	12.5
Lutjanidae					
Lutjanus sp., snapper		1		1	.9
Mugilidae					
Mugil cephalus, striped mullet	4	323	493	820	24.1
M. curema, white mullet	3	73	420	496	24.1
Stromateidae					
Peprilus sp., butterfish		2	1	3	1.8
Gerreidae					
Eucinostomus sp., mojarra	142	553	180	875	36.6
Sparidae					
Archosargus probatocephalus, sheepshead		2		2	1.8
Lagodon rhomboides, pinfish	27	7	1,216	1,250	18.8
Uranoscopidae					
Astroscopus y-graecum, southern stargazer		11	8	19	9.8

TABLE 2.—*Continued.*

Species	1975	1976	1977	Total	Frequency of occurrence
Pomacentridae					
Abudefduf saxatilis, sergeant major			18	18	.9
Lobotidae					
Lobotes surinamensis, tripletail	1	236	5	242	21.4
Blenniidae					
Hypsoblennius sp., blenny		22	2	24	6.3
Gobiidae					
Gobionellus hastatus, sharptail goby		1		1	.9
Ophidiidae					
Lepophidium sp., cusk eel		1		1	.9
Exocoetidae					
Hemiramphus brasiliensis, ballyhoo		3		3	1.8
Hyporhamphus unifasciatus, halfbeak	1	3	24	28	6.3
Belonidae					
Strongylura marina, Atlantic needlefish		3	1	4	1.8
Cyprinodontidae					
Fundulus similis, longnose killifish		2	2	4	3.6
Atherinidae					
Menidia beryllina, tidewater silverside	29	35	109	173	24.1
Membras martinica, rough silverside	180	5	317	502	17.9
Syngnathidae					
Syngnathus louisianae, chain pipefish	2	133	35	170	28.6
S. floridae, dusky pipefish	7	3	7	17	6.3
S. scovelli, gulf pipefish	5		2	7	2.7
Hippocampus zosterae, dwarf seahorse		1		1	.9
Sciaenidae					
Bairdiella chrysoura, silver perch		1	2	3	2.7
Cynoscion arenarius, sand seatrout		7		7	.9
C. nebulosus, spotted seatrout	1		2	3	2.7
Leiostomus xanthurus, spot	6	795	1,415	2,216	18.8
Menticirrhus littoralis, gulf kingfish	269	431	694	1,394	67.0
M. americanus, southern kingfish	19	213	40	272	25.9
M. saxatilis, king whiting	10	52	54	116	34.8
Larimus fasciatus, banded croaker		13	5	18	4.5
Micropogonias undulatus, Atlantic croaker		3		3	1.8
Carangidae					
Chloroscombrus chrysurus, Atlantic bumper	3	9	13	25	8.9
Trachinotus carolinus, Florida pompano	154	528	2,586	3,268	56.3
T. falcatus, permit		1		1	.9
Oligoplites saurus, leatherjacket	4	4	2	10	6.3
Caranx hippos, crevalle jack	2	56	14	72	11.6
Seriola zonata, banded rudderfish		1		1	.9
Selene vomer, lookdown		1		1	.9
Dactyloscopidae					
Dactyloscopus tridigitatus, sand stargazer			2	2	.9
Triglidae					
Prionotus tribulus, bighead searobin			1	1	.9
Cynoglossidae					
Symphurus plagiusa, blackcheek tonguefish		1		1	.9
Bothidae					
Citharichthys macrops, spotted whiff	3	16	4	23	6.3
Etropus sp., flounder		627	2	629	13.4
Paralichthys albigutta, gulf flounder		19	2	21	4.5
P. lethostigma, southern flounder	2	9	6	17	3.6
Tetraodontidae					
Sphoeroides sp., puffer		196	35	231	18.8
Balistidae					
Monacanthus hispidus, planehead filefish		39		39	4.5
Aluterus schoepfi, orange filefish		3		3	.9
Diodontidae					
Chilomycterus schoepfi, striped burrfish			1	1	.9
Totals	12,415	96,763	45,291	154,469	

Carangidae, and Sciaenidae. The dusky anchovy, *Anchoa lyolepis*, and the scaled sardine, *Harengula jaguana*, were numerically most important making up 80.2% of the total number of fishes collected. These species were abundant in all 3 yr, although *A. lyolepis* was most numerous in 1975 and 1977 and *H. jaguana* in 1976. The families Sciaenidae and Carangidae were represented by nine and seven species, respectively. The gulf kingfish, *Menticirrhus littoralis*, although only eighth in number, exhibited the highest frequency of occurrence (67%) of any species. The Florida pompano, *Trachinotus carolinus*, was the only carangid regularly occurring in the surf zone.

Relationships within two genera, *Sardinella* (Clupeidae) and *Menidia* (Atherinidae), are currently uncertain for the Gulf of Mexico. We followed Houde and Fore (1973) and Hoese and Moore

(1977) in recognizing the low anal ray count (generally 16) specimens of *Sardinella* sp. as Spanish sardine, *S. anchovia*. Our specimens of *Menidia* generally had three or fewer anal fin rays anterior to the posterior extension of the swim bladder by which Johnson (1975) characterized *M. peninsulae* (Goode and Bean). However, we have followed Edwards et al. (1978) in retaining tidewater silverside, *M. beryllina*, for this form.

Although some variation occurred in the annual ranking of species abundance (Table 3), *A. lyolepis*; *H. jaguana*; and gulf menhaden, *Brevoortia patronus*, were among the four most abundant species in all 3 yr. Less numerous species showed more variability. For instance, the striped anchovy, *A. hepsetus*, was third in abundance in 1976 but eighth in abundance in 1977, while *T. carolinus* was sixth in abundance in 1976 and fourth in abundance in 1977.

TABLE 3.—Rank order of abundance of the 10 most numerous fish species collected from the Horn Island, Miss., surf zone by year.

Species	1975	1976	1977
Anchoa lyolepsis	1	2	1
Harengula jaguana	2	1	2
Brevoortia patronus	3	4	3
Anchoa mitchilli	4	—	5
Anchoviella perfasciata	5	9	—
Menticirrhus littoralis	6	10	9
Membras martinica	7	—	—
Sardinella anchovia	8	—	—
Trachinotus carolinus	9	8	4
Eucinostomus sp.	10	7	—
Leiostomus xanthurus	—	5	6
Etropus sp.	—	6	—
Lagodon rhomboides	—	—	7
Anchoa hepsetus	—	3	8
Mugil cephalus	—	—	10

The number of fishes collected from the surf zone habitat of Horn Island was characterized by distinct seasonal changes. Peaks in fish per seine haul (collected between 0900 and 1600 h) occurred during the warmer months between June and September 1976 and 1977 (Figure 2). In 1975 fishes were not collected in large numbers until the August collection. Large numbers of fishes were collected as early as June in 1976 although few fishes were collected in July of the same year. In 1977 fishes were not collected in abundance in June, but were in July.

The number of fishes collected dropped during the fall and winter months but rose again during late winter and early spring (Figure 2). This secondary peak, occurring in March 1976 and 1977, was composed of denatant migrants (sensu Cushing 1975) which had recently been spawned

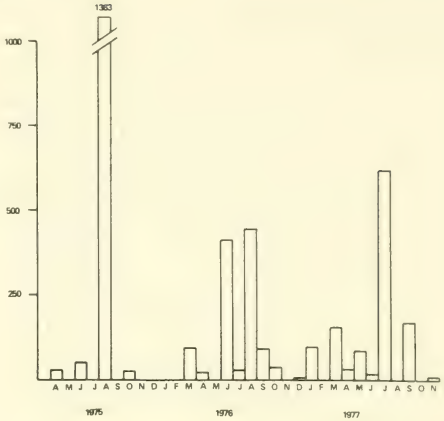


FIGURE 2.—Mean number of fishes collected per seine haul from Stations 1 through 4 on Horn Island, Miss., between April 1975 and November 1977. Data represents collections made between 0900 and 1600 h c.s.t.

offshore and were drifting into Mississippi Sound via the barrier island passes. Following the late winter (March) peak there was another period of low catch per effort between April and June in 1976 and 1977.

The numerically dominant species collected within the surf zone exhibited distinct seasonal occurrence patterns. Cluster analysis among these species indicated three modes of occurrence (Figure 3). Although data for the cluster analysis included only fishes collected between 0900 and 1600 h, there was no significant difference (χ^2, 5% level) in the monthly presence of fish species collected at this time period and those collected between 1600 and 0900 h. The most numerous species, *A. lyolepis* and *H. jaguana*, showed the highest similarity in seasonal occurrence and were most common during spring and summer. Other species also characteristic of spring and summer included *Eucinostomus* sp. and *T. carolinus*. *Anchoa hepsetus* and *Menticirrhus littoralis* had less seasonal affinity with the above species since they also occurred well into fall.

A second seasonal group included flat anchovy, *Anchoviella perfasciata*; *S. anchovia*; and white mullet, *Mugil curema*, which were representatives of the summer fauna (Figure 3). These species were never collected at water temperatures below 24.5° C.

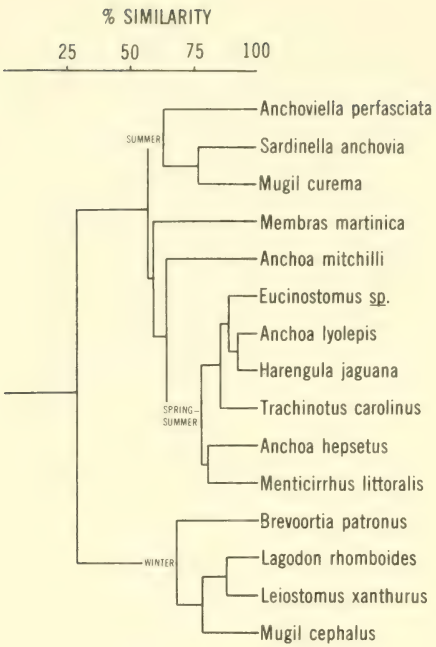


FIGURE 3.—Similarity dendrogram for species by month, based on presence or absence data, for fishes collected from the surf zone of Horn Island, Miss.

The third seasonal species group, *B. patronus*; pinfish, *Lagodon rhomboides*; spot, *Leiostomus xanthurus*; and striped mullet, *Mugil cephalus*, was prevalent during winter or early spring, generally in water temperatures below 24.5° C, with the first three occurring at temperatures as low as 11.5° C. Together these four species composed the secondary abundance peak of March 1976 and 1977 (cf. Figure 2).

Rough silverside, *Membras martinica*, and bay anchovy, *Anchoa mitchilli*, did not fit within the three seasonal categories. *Anchoa mitchilli* was collected in greatest abundance during the spring and in the fall, while *M. martinica* was most common in the spring, but only during 1975 and 1977. *Membras martinica* was infrequent in 1976.

Multiple regression analysis explained little of the variation associated with fish abundance (i.e., fish per seine haul). However, while tentative, the analysis may indicate the relative importance of these variables in controlling fish occurrence (Table 4). The dominant factor affecting the clupeiform fishes was tide level. Tide contributed only 5.1% and 8.9% in the regression equations for *H. jaguana* and *A. hepsetus*, and accounted for 19.2% of the model for *A. lyolepis* ($P<0.05$). The remaining variables contributed little to the predictive ability of the regression equations, although salinity composed 5.6% of the variance model for *A. hepsetus* ($P<0.05$). Temperature was the dominant parameter in the model for *T. carolinus* (not significant) and *Menticirrhus littoralis* ($P<0.05$).

While not apparent from Table 4, our observations indicate that catch per effort (cf. Figure 2) may coincide with wind direction. Wind patterns in the study area undergo annual cycles in which direction is primarily from the north during the winter and from the south during the summer. Fishes were collected in greatest numbers during the summer when southerly winds predominated.

Daily Activity Patterns

The greatest number of fishes were present within the surf zone during the early morning

TABLE 4.—Stepwise multiple regression of the five major environmental parameters contributing to the average number of fish collected per seine haul in the surf zone of Horn Island, Miss.

Species and parameter	Cumulative R	R^2	Cumulative R^2	F	df
Anchoa lyolepis					
Tide	0.438	0.192	0.192	15.72*	6, 75
Wave height	.452	.012	.205	.16	
Wind direction	.457	.005	.209	.23	
Temperature	.461	.003	.212	.22	
Wind speed	.462	.001	.213	.06	
Harengula jaguana					
Tide	.227	.051	.051	3.96*	5, 76
Temperature	.255	.014	.065	.82	
Wind direction	.274	.010	.075	.69	
Salinity	.278	.002	.077	.20	
Wave height	.279	.001	.078	.06	
Anchoa hepsetus					
Tide	.297	.089	.089	8.96*	6, 76
Salinity	.380	.056	.144	5.00*	
Temperature	.398	.014	.158	.90	
Wind direction	.411	.011	.169	1.00	
Slope	.415	.003	.172	.32	
Trachinotus carolinus					
Temperature	.199	.040	.040	2.14	7, 74
Salinity	.241	.018	.058	1.02	
Wind speed	.254	.007	.065	.93	
Tide	.262	.004	.068	.68	
Wind direction	.268	.004	.072	.60	
Menticirrhus littoralis					
Temperature	.309	.095	.095	8.62*	6, 75
Tide	.329	.013	.108	.77	
Salinity	.333	.002	.111	.21	
Wave height	.334	.001	.112	.52	
Slope	.338	.002	.113	.38	

*Significant ($P<0.05$).

(0300-0900) for all six 24-h samples made in 1976 (Figure 4). From May to September, excluding August when diel collections were not taken, fishes exhibited a distinct rise in abundance between 0300 and 0600 h c.s.t. with peak occurrences just after sunrise. The number of fishes collected during this time period far exceeded those captured during the later daylight hours; in June no collection was made during this time period.

The daily pattern of catch per effort reflected the numerical dominance of *H. jaguana* and *A. lyolepis*. The greatest number of fish for both species was collected during the early morning with a subsequent decline throughout the day (Figure 5). Peak capture rates for *H. jaguana* and *A. lyolepis* were 1,712 and 2,339 fish/seine haul, whereas the lowest mean rates were 6 and 0.1 fish/seine haul during the 1200-1500 h period for *H. jaguana* and the 1800-2100 h period for *A. lyolepis*. A secondary peak in abundance occurred between 1500 and 1800 h with 252 and 545 fish collected per seine haul for *H. jaguana* and *A. lyolepis*. High numbers of *A. hepsetus* also occurred during the morning; however, peak catch per effort occurred between 0600 and 0900 h. This species was less abundant than *H. jaguana* and *A. lyolepis*, with only 33 fish collected per seine haul. *Anchoa hepsetus* remained within the beach area through 1200-1500 h, but no fish were captured between 1500 and 1800 h.

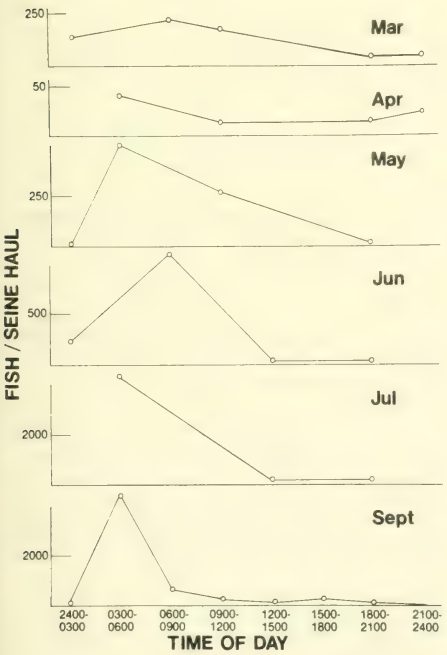


FIGURE 4.—Monthly mean number of fish per seine haul collected during the designated time intervals from the surf zone of Horn Island, Miss., between March and September 1976, excluding August.

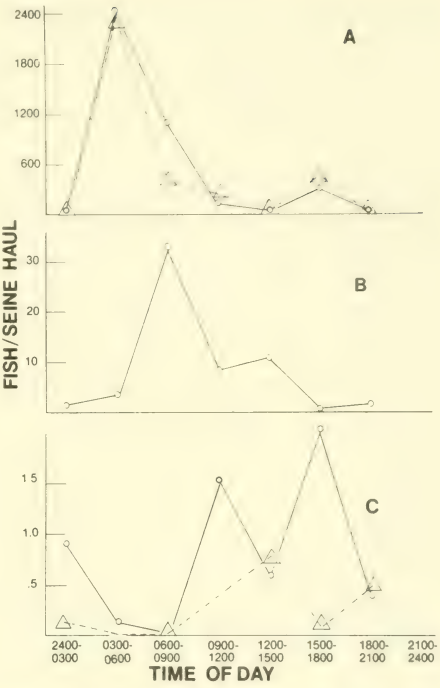


FIGURE 5.—Daily changes of mean number of fish per seine haul for the Horn Island, Miss., surf zone (April 1976-September 1976). Data are for the numerically most important species. A = *Anchoa lyolepis* (broken line) and *Harengula jaguana* (solid line). B = *Anchoa hepsetus*. C = *Trachinotus carolinus* (broken line) and *Menticirrhus littoralis* (solid line).

Menticirrhus littoralis and *T. carolinus* did not exhibit distinct daily activity patterns, but tended to be more abundant during midafternoon or evening. The greatest number of *M. littoralis* collected was only 2.0 fish/seine haul between 1800 and 2100 h while the greatest number of

T. carolinus per seine haul was 0.8 fish between 1500 and 1800 h.

DISCUSSION

Species Composition

The ichthyofauna of the Horn Island surf zone resembles that of other surf zone habitats within the Gulf of Mexico. Using similar collecting gear, Gunter (1958) reported that over a 3-yr period *T. carolinus* and *H. pensacolae* (= *H. jaguana*) were the numerical dominants from the surf zone of Mustang Island, Texas. McFarland (1963), using a much larger seine (193 m long with 1.9 cm mesh), found that *Mugil cephalus* and Atlantic threadfin, *Polydactylus octonemus*, were dominant by weight and number, respectively, of the same area. While fishes collected by McFarland were generally >100 mm, many of the same species were collected by Gunter (1958) and in our study as larvae and juveniles.

Springer and Woodburn (1960) described a faunal assemblage for the surf habitat (exposed beach) near Tampa Bay, Fla., which was very similar to that of Horn Island. *Harengula jaguana* was the numerically dominant species collected during the warmer months, followed numerically by *Lagodon rhomboides* and *Menticirrhus littoralis*.

Although a numerically dominant species in the present study, *Anchoa lyolepis* has never been reported as common within a Gulf of Mexico coastal surf habitat. Gunter (1958) reported that *A. lyolepis* was taken only occasionally in the surf zone of Mustang Island, and Naughton and Saloman (1978) found it to be rare in a western Florida surf area. Springer and Woodburn (1960) collected only *A. hepsetus* and *A. mitchilli* from exposed beaches near Tampa Bay. Daly (1970) found *A. nasuta* (synonymized with *A. lyolepis* by Whitehead 1973) to be uncommon on the western tip of south Florida, although it ranges from Cape Hatteras, N.C., into the Gulf of Mexico through the West Indies to the Gulf of Venezuela (Daly 1970). In Mississippi Sound, Christmas and Waller (1973) occasionally collected *A. nasuta* of 36-59 mm SL in higher salinity water (20.0-35.5‰). Their data, based on several years of observation, indicated that *A. nasuta* occurred only in the summer and fall and was never abundant.

In comparing latitudinal variation of surf zone ichthyofaunas Gunter (1958) suggested that the major species occupying the Texas beach were the same or cognates to species observed in North Carolina which were cognates to those reported from New England beaches. Springer and Woodburn (1960) acknowledged that certain similarities existed within broad geographical ranges; however, they pointed out that many dissimilarities existed between temperate and tropical faunas within the eastern United States.

Between-study comparisons are made difficult due to differences in sizes of collecting gear and sampling designs. For instance, McFarland (1963) stated that the small clupeids, particularly the scaled sardine and engraulids, were undersampled because his collecting gear generally eliminated fishes <40 mm SL. However, for the warm-temperate to tropical regions of the Atlantic and Gulf of Mexico there seems to be a very characteristic species assemblage utilizing surf zone areas. Species listed as numerically important in both warm-temperate to tropical Gulf of Mexico and western Atlantic studies (Table 5) were *A. mitchilli*, *A. lyolepis* (= *A. nasuta*), *T. carolinus*, *M. littoralis*, and *H. jaguana* (= *H. pensacolae*). In addition, Atlantic silverside, *Menidia menidia*, and Atlantic menhaden, *B. tyrannus*, in the Atlantic and *M. beryllina* and *B. patronus* in the Gulf were numerically important. *Harengula jaguana* was most frequently reported as numerically dominant along Gulf of Mexico beaches; only Gilmore (1977) found it to have high abundance in the Atlantic surf zone off the Indian River area of Florida. However, the northern limit of this species is in the area of Cape Kennedy on the Florida Atlantic coast (Rivas 1963). Gilmore (1977) also found *A. nasuta* to be abundant in the surf zone along the eastern Florida coast. While *Menticirrhus littoralis* was not among the five most abundant species in some Gulf of Mexico studies (including ours), its high frequency of occurrence in our study indicates that it is an important surf zone species. Based on Table 5, atherinids, primarily of the genus *Menidia*, were more often among the five most abundant species collected in the Atlantic (seven out of nine studies) than Gulf of Mexico surf zones (two out of six studies).

Seasonal and Annual Variations

Temporal changes in both abundance and composition were primary characteristics of the ichthyofauna utilizing surf zone habitats of Horn Island. Fishes collected in our study were most

TABLE 5.— List of the first five numerically abundant fish species collected from the surf zone habitat of marine sandy beaches of the Gulf of Mexico and temperate Atlantic coast states.

Region	Major species	Total no. of species	Reference
Gulf coast:			
Mustang Island, Texas	*Trachinotus carolinus, Harengula jaguana, Mugil curema, Anchoa mitchilli, Micropogonias undulatus*	44	Gunter (1958)
Mustang Island, Texas	*Polydactylus octonemus, Menidia beryllina, Mugil cephalus, Menticirrhus littoralis, Chloroscombrus chrysurus*	48	McFarland (1963)
Gilchrist, Texas	*Brevoortia patronus,*[1] *Anchoa mitchilli, Polydactylus octonemus, Arius felis, Chloroscombrus chrysurus, Trachinotus carolinus*	25	Reid (1955b)
Horn Island, Miss.	*Anchoa lyolepis, Harengula jaguana, Brevoortia patronus, Anchoa hepsetus Trachinotus carolinus*	76	Present study
Panama City, Fla	*Harengula jaguana, Menidia beryllina, Lagodon rhomboides, Trachinotus carolinus, Mugil curema*	44	Naughton and Saloman (1978)
Tampa Bay, Fla.	*Harengula jaguana, Lagodon rhomboides, Menticirrhus littoralis, Leiostomus xanthurus, Trachinotus carolinus*	47	Springer and Woodburn (1960)
East coast:			
Indian River, Fla.	*Harengula jaguana, Ophisthonema oglinum, Sardinella anchovia, Anchoa hepsetus, A. mitchilli, A. nasuta*[2]	78	Gilmore (1977)
Statewide, South Carolina	*Menidia menidia, Anchoa mitchilli, Trachinotus carolinus, Menticirrhus littoralis, Anchoa hepsetus*	39	Cupka (1972)
Folly Island, S.C.	*Menidia menidia, Anchoa hepsetus, Menticirrhus littoralis, Trachinotus carolinus, Mugil curema*	43	Anderson et al. (1977)
Beaufort, N.C.	*Menidia menidia, Anchoa mitchilli, Trachinotus carolinus, Menticirrhus* sp., *Fundulus majalis*	8	Pearse et al. (1942)
Beaufort, N.C.	*Brevoortia tyrannus, Anchoa hepsetus, Membras martinica, Lagodon rhomboides, Menticirrhus littoralis*	40	Tagatz and Dudley (1961)
Fire Island, N.Y.	*Sphoeroides maculatus, Alosa aestivalis, Poronotus triacanthus, Morone saxatilis, A. mediocris*	71	Schaefer (1967)
Long Island, Conn.	*Menidia menidia, Fundulus majalis, Menidia* sp. (immature), *Brevoortia tyrannus, Fundulus heteroclitus*	35	Hillman et al. (1977)
Pine Orchard, Conn.	*Menidia menidia, Sphoeroides maculatus, Brevoortia tyrannus, Pseudopleuronectes americanus, Syngnathus peckianus*	13	Merriman (1947)
Morris Cove, Conn.	*Menidia menidia, Brevoortia tyrannus, Syngnathus fuscus, Clupea harengus. Pseudopleuronectes americanus*	32	Warfel and Merriman (1944)

[1]Abundance of *Brevoortia patronus* was considered distorted due to the coincidence of a large school of adults moving inshore during the sampling effort
[2]Equal numbers of *Anchoa mitchilli* and *A. nasuta* collected.

abundant during the summer, although the onset of high fish density varied somewhat between years. High numbers of fishes first appeared in June in 1976, but not until August in 1975 and July in 1977. Annual variability in the time of peak catch may be due, in part, to short-term variation in local water conditions. The low numbers of fishes collected in July 1976 may have been due to unusually calm and clear water which increased net avoidance. Large numbers of fishes were collected during the predawn hours of July 1976, indicating that fishes were abundant along the beach during this period.

Similar changes in the abundance of surf zone fishes have been observed in other studies. Gunter (1958) reported that fishes occupying the exposed beach of Mustang Island underwent seasonal succession during which fish abundance was greatest during the summer and least in the winter. Seasonal changes in abundance were also reported by Springer and Woodburn (1960), McFarland (1963), Schaefer (1967), and Anderson et al. (1977). McFarland (1963) proposed four categories of seasonal occurrence for surf zone fishes: all-year residents, spring-summer residents, summer residents, and winter residents. Of the major species common to both McFarland's study and ours, sea catfish, *Arius felis*; *Mugil cephalus*; and *L. rhomboides* were considered as all-year residents, whereas *H. jaguana*; *Anchoa* sp.; *T. carolinus*; *Menticirrhus littoralis*; king whiting, *M. saxatilis*; and southern kingfish, *M. americanus*, were classified as spring-summer residents. McFarland noted, as we have, that fishes characteristic of the spring and summer dominated the numerical component of the ichthyofauna.

The influx of denatant migrants collected within the surf zone during the winter in our study has not been reported previously. However, the annual movement of larval menhaden and sciaenids into estuaries along the Gulf of Mexico and Atlantic coasts during the winter is well documented (Gunter 1967; Dahlberg 1972; Christmas and Waller 1973). These species likely did not utilize the surf zone specifically, but were concentrated along the island before moving through the barrier island passes. Therefore, their appearance within the surf zone habitat appears dependent

more upon wind and current movements rather than habitat preference.

Throughout our study *A. lyolepis* and *H. jaguana* clearly dominated the numerical component of the surf zone ichthyofauna; however, differences in the rank of the remaining species did occur. Gunter (1958) suggested that intraseason species abundance in the surf zone of Mustang Island changed annually, although *T. carolinus* and *H. jaguana* were generally present in considerable numbers. Reid (1956) observed that the greater number of the surf zone ichthyofauna along the Texas coast, with the exception of *B. patronus*, was similar during successive summers. Star drum, *Stellifer lanceolatus*, was considerably more abundant during the second summer as were *T. carolinus*, *M. littoralis*, and *M. americanus*. During the first summer of a 3-yr study, Schaefer (1967) observed butterfish, *Peprilus triacanthus*, as the numerically dominant species within the surf zone of Fire Island, N.Y. In the remaining two summers of his study, northern puffer, *Sphoeroides maculatus*, was the most numerous species.

Factors Affecting Occurrence

The dominant factors affecting the abundance of fishes within the surf zone of Horn Island were tide level, time of day, and temperature. The frequency of engraulids and clupeids was closely associated with time and tide. However, during the summer sampling periods, when fish abundance was greatest in the early morning, tide levels were also highest. Consequently, the effect of the two factors is difficult to separate. Subsequent research (Ross unpubl. data) indicates that both may be important, although Roessler (1970) found that the frequency of *H. jaguana* collected from southern Florida was not significantly related to tidal fluctuation. Seasonal changes in temperature appeared to be of most importance in affecting the frequency of *T. carolinus* and *M. littoralis*.

The pronounced daily variation in occurrence of the most abundant fishes (i.e., *A. lyolepis*, *A. hepsetus*, and *H. jaguana*) indicates that they are not as permanently associated with the surf zone habitat as the gulf kingfish and the Florida pompano. Diel catch rates showed that engraulids and clupeids largely moved out of the surf zone during the day, whereas, the gulf kingfish and Florida pompano exhibited little change in daily abundance. Predator avoidance may be an important reason for the high early morning densities of the clupeoid fishes.

Other studies have also documented the influence of time of day and tidal cycle on fish abundance in surf areas. Merriman (1947) found that shore zone fishes in Connecticut had activity patterns associated with tide level. The greatest number of fishes occurred during high tide when fish appeared to be actively feeding. Daly (1970) also described daily activity patterns in anchovies collected along south Florida beaches. Anderson et al. (1977) suggested that temperature was the primary factor affecting fish abundance along a South Carolina beach; however, diel changes were not investigated. de Sylva et al. (footnote 3) also found that temperature was the greatest factor in determining frequency of most fishes, whereas salinity was secondary in importance and turbidity had little effect. The importance of temperature and salinity to the abundance and distribution of fishes has been discussed in depth by Gunter (1938, 1945, 1950, 1957) and to some extent by Warfel and Merriman (1944). Warfel and Merriman reported that the greatest and lowest number of fishes appeared relative to high and low temperatures, but that no direct correlation could be made. Gunter (1945, 1957) suggested that temperature was the dominant factor in initiating seasonal migrations and other cyclic activities of fishes along the Texas coast. The interaction of wind direction (i.e., inshore winds) with temperature may further increase the number of fishes in the Horn Island surf zone.

In summary, the Horn Island surf zone is utilized primarily by *H. jaguana*, *A. lyolepis*, *A. hepsetus*, *M. littoralis*, and *T. carolinus*. There is strong seasonal periodicity with the greatest abundance in spring and summer, as well as daily fluctuations due to tide level and time of day. Since the individuals of the above species were primarily late larval and juvenile forms, the importance of surf zone habitats as nursery and refuge areas for certain species should be recognized.

ACKNOWLEDGMENTS

We wish to express our appreciation to Kathleen Clark and John Baker for their consistent willingness to assist in the field. We are also indebted to Harriet Perry and her staff at the Gulf Coast Research Laboratory for the use of their facilities and equipment, and to the National Park Service for allowing us to collect on Horn Island. Wind

data were provided by the Physical Oceanography Section of the Gulf Coast Research Laboratory. We thank Sally L. Richardson for her constructive comments on an earlier draft of the manuscript.

Financial aid during this study was provided by two Sigma Xi Grants-In-Aid of Research (to T. Modde) and by the University of Southern Mississippi Biology Department. This study is adapted from a portion of a doctoral dissertation submitted by T. Modde to the Biology Department of the University of Southern Mississippi.

LITERATURE CITED

ANDERSON, W. D., JR., J. K. DIAS, R. K. DIAS, D. M. CUPKA, AND N. A. CHAMBERLAIN.
1977. The macrofauna of the surf-zone off Folly Beach, South Carolina. U.S. Dep. Commer., NOAA Tech. Rep., NMFS SSRF-704, 23 p.

CHRISTMAS, J. Y., AND R. S. WALLER.
1973. Estuarine vertebrates, Mississippi. *In* J. Y. Christmas (editor), Cooperative Gulf of Mexico Estuarine Inventory and Study, Mississippi, p. 320-406. Gulf Coast Res. Lab., Ocean Springs, Miss.

CUPKA, D. M.
1972. A survey of the ichthyofauna of the surf-zone in South Carolina. S.C. Wildl. Mar. Resour. Cent., Tech. Rep. 4, 19 p.

CUSHING, D. H.
1975. Marine ecology and fisheries. Camb. Univ. Press, 278 p.

DAHLBERG, M. D.
1972. An ecological study of Georgia coastal fishes. Fish. Bull., U.S. 70:323-353.

DALY, R. J.
1970. Systematics of southern Florida anchovies (Pisces: Engraulidae). Bull. Mar. Sci. 20:70-104.

EDWARDS, R. J., E. MARSH, AND F. B. STEVENS, JR.
1978. The utility of the air bladder position in determining specific relationships in the atherinid genus *Menidia*. Contrib. Mar. Sci. 21:1-7.

GILMORE, R. G., JR.
1977. Fishes of the Indian River lagoon and adjacent waters, Florida. Bull. Fla. State Mus., Biol. Sci. 22: 101-148.

GUNTER, G.
1938. Seasonal variations in abundance of certain estuarine and marine fishes in Louisiana with particular reference to life histories. Ecol. Monogr. 8:313-346.
1945. Studies on marine fishes of Texas. Publ. Inst. Mar. Sci., Univ. Tex. 1:1-190.
1950. Correlation between temperature of water and size of marine fishes on the Atlantic and Gulf coasts of the United States. Copeia 1950:298-304.
1957. Temperature. *In* J. W. Hedgpeth (editor), Treatise on Marine Ecology and Paleoecology, Vol. 1, p. 159-184. Geol. Soc. Am. Mem. 67.
1958. Population studies of the shallow water fishes of an outer beach in south Texas. Publ. Inst. Mar. Sci. Univ. Tex. 5:186-193.
1967. Some relationships of estuaries to the fisheries of the Gulf of Mexico. *In* G. H. Lauff (editor), Estuaries, p. 621-638. Am. Assoc. Adv. Sci. Publ. 83, Wash., D.C.

HILLMAN, R. E., N. W. DAVIS, AND JAY WENNEMER.
1977. Abundance, diversity, and stability in shore-zone fish communities in an area of Long Island Sound affected by the thermal discharge of a nuclear power station. Estuarine Coastal Mar. Sci. 5:355-381.

HOESE, H. D., AND R. H. MOORE.
1977. Fishes of the Gulf of Mexico: Texas, Louisiana and adjacent waters. Texas A&M Univ. Press, College Station, 327 p.

HOUDE, E. D., AND P. L. FORE.
1973. Guide to identity of eggs and larvae of some Gulf of Mexico clupeid fishes. Fla. Dep. Nat. Resour., Mar. Res. Lab., Leafl. Ser. 4(23), 14 p.

JOHNSON, M. S.
1975. Biochemical systematics of the atherinid genus *Menidia*. Copeia 1975:662-691.

MCFARLAND, W. N.
1963. Seasonal change in the number and the biomass of fishes from the surf at Mustang Island, Texas. Publ. Inst. Mar. Sci., Univ. Tex. 9:91-105.

MERRIMAN, D.
1947. Notes on the midsummer ichthyofauna of a Connecticut beach at different tide levels. Copeia 1947: 281-286.

NAUGHTON, S. P., AND C. H. SALOMAN.
1978. Fishes of the nearshore zone of St. Andrew Bay, Florida, and adjacent coast. Northeast Gulf Sci. 2:43-55.

ODUM, E. P.
1971. Fundamentals of ecology. 3d ed. Saunders, Phila., 574 p.

ODUM, H. T., AND B. J. COPELAND.
1974. A functional classification of the coastal systems of the United States. *In* H. T. Odum, B. J. Copeland, and E. A. McMahan (editors), Coastal ecological systems of the United States. Vol. 1, p. 5-84. The Conservation Foundation, Wash., D.C.

PEARSE, A. S., H. J. HUMM, AND G. W. WHARTON.
1942. Ecology of sand beaches at Beaufort, North Carolina. Ecol. Monogr. 12:135-140.

REID, G. K.
1956. Observations in the eulittoral ichthyofauna of the Texas Gulf coast. Southwest. Nat. 1:157-165.

REID, G. K., JR.
1955a. A summer study of the biology and ecology of East Bay, Texas. Part I. Introduction, description of area, methods, some aspects of the fish community, the invertebrate fauna. Tex. J. Sci. 7:316-343.
1955b. A summer study of the biology and ecology of East Bay, Texas. Part II. The fish fauna of East Bay, the Gulf beach, and summary. Tex. J. Sci. 7:430-453.

RIVAS, L. R.
1963. Genus *Harengula* Cuvier and Valenciennes 1847 Sardines. *In* Y. H. Olsen (editor), Fishes of the western North Atlantic. Part three, p. 386-396. Mem. Sears Found. Mar. Res. 1.

ROESSLER, M. A.
1970. Checklist of fishes in Buttonwood Canal, Everglades National Park, Florida, and observations on the seasonal occurrence and life histories of selected species. Bull. Mar. Sci. 20:860-893.

SCHAEFER, R. H.
1967. Species composition, size and seasonal abundance of fish in the surf waters of Long Island. N.Y. Fish Game J. 14:1-46.

SNEATH, P. H. A., AND R. R. SOKAL.
1973. Principle of numerical taxonomy. W. H. Freeman and Co., San Fran., 573 p.

SPRINGER, V. G., AND K. D. WOODBURN.
1960. An ecological study of the fishes of the Tampa Bay area. Fla. State Board Conserv., Mar. Lab., Prof. Pap. Ser. 1, 104 p.

TAGATZ, M. E., AND D. L. DUDLEY.
1961. Seasonal occurrence of marine fishes in four shore habitats near Beaufort, North Carolina, 1957-1960. U.S. Fish. Wildl. Serv., Spec. Sci. Rep. Fish. 390, 19 p.

WARFEL, H. E., AND D. MERRIMAN.
1944. Studies on the marine resources of southern New England. I. An analysis of the fish population of the shore zone. Bull. Bingham Oceanogr. Collect. Yale Univ. 9:1-91.

WHITEHEAD, P. J. P.
1973. The clupeoid fishes of the Guianas. Bull. Br. Mus. Nat. Hist. (Zool.) Suppl. 5:1-227.

LARVAL DEVELOPMENT OF PACIFIC TOMCOD, *MICROGADUS PROXIMUS*, IN THE NORTHEAST PACIFIC OCEAN WITH COMPARATIVE NOTES ON LARVAE OF WALLEYE POLLOCK, *THERAGRA CHALCOGRAMMA*, AND PACIFIC COD, *GADUS MACROCEPHALUS* (GADIDAE)

ANN C. MATARESE,[1] SALLY L. RICHARDSON,[2] AND JEAN R. DUNN[1]

ABSTRACT

A developmental series from yolk-sac larvae through juveniles (2.7-46.6 mm SL) of *Microgadus proximus* from the northeast Pacific Ocean is described and illustrated. Larvae hatch at approximately 2.7 mm SL and the yolk is absorbed by 3.0 mm SL. Notochord flexion begins between 8.0 and 10.0 mm SL, is completed at 15.0 mm SL, and transformation occurs between 22.0 and 28.0 mm SL. Larvae have specific pigment patterns, particularly in the postanal region where melanophores are arranged in two bars, anterior and posterior. At 5.0-6.0 mm SL, the anterior bar is located at 41-53% SL and the posterior bar is at 61-74% SL. Melanophore patterns on the head, gut, and caudal region also distinguish *M. proximus*. The occurrence of larvae taken within 18 km of shore off Oregon during plankton surveys in 1971-72 is discusssed, and data indicate a winter-spring spawning period.

A combination of pigmentation characters, primarily the length and position of the anterior and posterior pigment bars, and meristic counts can distinguish larvae of *M. proximus* from *Theragra chalcogramma* and *Gadus macrocephalus*. The anterior bar is located at 47-55% SL in *T. chalcogramma* and at 40-57% SL in *G. macrocephalus*. The posterior bar is located at 69-79% SL in *T. chalcogramma* and at 59-81% SL in *G. macrocephalus*. Both *T. chalcogramma* and *G. macrocephalus* have 4 rays on the superior hypural element while *M. proximus* has 5 rays. Other characters useful in separating the three species include head, gut, mediolateral, postanal, and caudal pigment and stripe continuity.

Problems have been encountered in distinguishing larvae of Pacific tomcod, *Microgadus proximus* (Girard); walleye pollock, *Theragra chalcogramma* (Pallas); and Pacific cod, *Gadus macrocephalus* (Tilesius), in samples from the northeastern Pacific Ocean where these three species might cooccur (Waldron 1972; Dunn and Naplin[3]). Larvae of *T. chalcogramma* were described by Gorbunova (1954) and Yusa (1954). Larvae of *G. (morhua) macrocephalus* larvae were described by Gorbunova (1954), Uchida et al. (1958), and Mukhacheva and Zviagina (1960). In this report we provide the first published description of the larvae of *M. proximus* and comparative material on larvae of *T. chalcogramma* and *G. macrocephalus* that should enable workers to identify larvae of these three gadids in mixed samples. Eggs and larvae of the Atlantic tomcod, *Microgadus tomcod*, were described by Booth (1967), but eggs of *M. proximus* are unknown.

The geographic range of *M. proximus* extends from off central California (Isaacson 1965) to the Gulf of Alaska and Unalaska Island (Wilimovsky 1964). Their presence in the Bering Sea remains unconfirmed, although they were reported to occur in the Bering Sea by Tanner (1894) and Hart (1973). *Microgadus proximus* was not captured in the eastern Bering Sea during extensive multivessel groundfish surveys in 1974 (Pereyra et al.[4]) or in 1976 (Bakkala and Smith[5]). *Microgadus proximus* is found from near-surface waters to ap-

[1]Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112.

[2]Gulf Coast Research Laboratory, East Beach Drive, Ocean Springs, MS 39564.

[3]Dunn, J. R., and N. A. Naplin. 1974. Fish eggs and larvae collected from waters adjacent to Kodiak Island, Alaska, during April and May, 1972. Unpubl. manuscr., 61 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112.

[4]Pereyra, W. T., J. E. Reeves, and R. G. Bakkala. 1976. Demersal fish and shellfish resources of the eastern Bering Sea in the baseline year 1975. Unpubl. manuscr., Vol. 1, 619 p.; Vol. 2, 534 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112.

[5]Bakkala, R. G., and G. B. Smith. 1978. Demersal fish resources of the eastern Bering Sea: Spring 1976. Unpubl. manuscr., Vol. 1, 234 p.; Vol. 2, 404 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112.

Manuscript accepted May 1980.
FISHERY BULLETIN: VOL. 78, NO. 4, 1981.

proximately 220 m (Miller and Lea 1972). Planktonic larvae of *M. proximus* were the dominant gadid and fourth most abundant taxon in a coastal assemblage of fish larvae occurring off Yaquina Bay, Oreg., in 1971-72 (Richardson and Pearcy 1977).

Information on the biology and taxonomy of *M. proximus* is limited. Schultz and Welander (1935) presented counts of meristic structures and morphological measurements of *M. proximus*. Svetovidov (1948), in his review of Gadiformes, provided some meristic data and a brief osteological description of *M. proximus* based on two skeletons. Brief notes on the biology of the species are included in Clemens and Wilby (1961), Miller and Lea (1972), and Hart (1973). It is not of commercial importance in part because of its small size (to 30 cm) but it is taken in recreational catches (Beardsley and Bond 1970; Hart 1973).

METHODS

Specimens

Several hundred larvae of the three species were examined in the course of this study. *Microgadus proximus* larvae and juveniles were obtained from plankton and trawl samples collected off Oregon in 1971-1973 and 1979, by the School of Oceanography, Oregon State University (OSU), Corvallis, and off Washington in 1972 by the Northwest and Alaska Fisheries Center (NWAFC). Additional specimens were obtained from plankton collected in Puget Sound, Wash., in 1977-79 by the Fisheries Research Institute (FRI), University of Washington, Seattle; and in 1978 by Ecology Consultants, Inc., Fort Collins, Colo. Larvae were also collected from near Kodiak Island, Alaska, in 1977-79 by FRI.

Theragra chalcogramma larvae were collected in the eastern Bering Sea (1971, 1976-78) and off Kodiak Island (1972, 1977-78) by NWAFC. Additional specimens from Puget Sound, Wash., (1977, 1978) were provided by FRI and by Ecology Consultants, Inc., and from off Kodiak Island (1978) by FRI.

Gadus macrocephalus larvae were collected near Kodiak Island in 1978 by NWAFC and FRI and from Puget Sound, Wash., in 1977-79 by FRI.

Radiographs were examined of juvenile and adult *M. proximus* and *G. macrocephalus* specimens in the collections in the Department of Fisheries and Wildlife, OSU, and NWAFC, and of adult *T. chalcogramma* specimens at NWAFC and from the Institute of Animal Resource Ecology, University of British Columbia, Vancouver.

Illustrations of larvae were made with the aid of a camera lucida. All specimens had been preserved in either 3-5% Formalin,[6] buffered with sodium borate, or 95% ethanol. Illustrations of caudal fin development were drawn from cleared and stained specimens.

Measurements

The following measurements were made on 72 unstained larvae and juveniles (2.7-46.6 mm SL) of *M. proximus* using an ocular micrometer in a stereomicroscope:

Standard length (SL)—Snout tip to notochord tip prior to development of caudal fin, then to posterior margin of hypural element. (All body lengths in this study are standard lengths.)

Head length (HL)—Snout tip to posterior edge of opercle (to pectoral fin base in yolk sac and very small larvae before opercular margin is visible).

Snout length—Snout tip to anterior margin of orbit of left eye.

Upper jaw length—Snout tip to posterior margin of maxillary.

Eye diameter—Greatest diameter of left orbit.

Body depth at pectoral—Vertical distance from dorsal to ventral body margin at pectoral fin base.

Body depth at anus—Vertical distance from dorsal to ventral body surface at center of anal opening.

Snout to anus—Distance along body midline from snout tip to vertical through center of anal opening.

Snout to first dorsal fin—Distance along the body midline to vertical through origin of anteriormost dorsal fin ray of first dorsal fin.

Snout to second dorsal fin—Distance along body midline to vertical through origin of anteriormost fin ray of second dorsal fin.

Snout to third dorsal fin—Distance along body midline to vertical through origin of anteriormost fin ray of third dorsal fin.

Snout to first anal fin—Distance along body midline to vertical through origin of anteriormost fin ray of first anal fin.

[6]References to trade names do not imply endorsement by the National Marine Fisheries Service, NOAA.

Snout to second anal fin—Distance along body midline to vertical through origin of anteriormost fin ray of second anal fin.

Meristic Structures

Counts of meristic structures were made on 128 stained *M. proximus* larvae and juveniles. Sixty-six specimens (3.1-41.1 mm SL) were cleared and stained with Alizarin Red S (Taylor 1967), and 62 larvae (5.1-23.4 mm SL) were stained with Alizarin Red and Alcian Blue (Dingerkus and Uhler 1977). Both series of stained samples were used to make counts of meristic structures and to determine the onset and sequence of ossification as indicated by the uptake of Alizarin Red. Structures, including teeth, were considered ossified even if only slightly stained with Alizarin Red.

Counts on stained larvae and early juveniles were made of first, second, and third dorsal fin rays, first and second anal fin rays, caudal fin rays, left pectoral and pelvic fin rays, branchiostegal rays, gill rakers, abdominal and caudal vertebrae (including the postural centrum), and neural and haemal spines. Counts were made of premaxillary and dentary teeth on 12 specimens (11.9-41.1 mm SL).

Counts of meristic structures of juveniles and adults of *M. proximus*, *T. chalcogramma*, and *G. macrocephalus* were made from radiographs. Counts were made of first, second, and third dorsal fin rays, first and second anal fin rays, caudal fin rays, and abdominal and caudal vertebrae (including the postural centrum).

IDENTIFICATION OF *MICROGADUS PROXIMUS*

A developmental series of *M. proximus* specimens ranging from late yolk-sac larvae to early juveniles was linked by pigment patterns, myomere counts, fin development, and meristic counts in larger specimens. They were identified as gadids based on three criteria: 1) Distinctive pigment patterns, which in small larvae consist of an anterior and posterior pigment bar, each composed of a dorsal and ventral stripe. With further growth of larvae, these bars diffuse into dorso- and ventrolateral rows of pigment accompanied by development of a mediolateral line of melanophores. 2) Relatively high (54-58) myomere counts. 3) Presence of a "pseudocaudal" fin (Ahlstrom and Counts 1955) at about 8.5 mm SL, as indicated by the development of dorsal and ventral procurrent caudal rays before the development of hypurals.

Considering the collection locations (coastal Oregon and Washington) and the range of myomere counts, the specimens could have been one of only three potential species, *M. proximus*, *T. chalcogramma*, or *G. macrocephalus*. Meristic characters in the literature (e.g., Svetovidov 1948; Miller and Lea 1972; Hart 1973) are inadequate to separate all three species. Additional counts obtained in this study, particularly caudal vertebrae and fin rays on the superior hypural (Tables 1, 2), enabled positive identification of the series as *M. proximus*.

DEVELOPMENT OF *MICROGADUS PROXIMUS*

Pigment Patterns (Figures 1, 2)

Pigmentation varies in *M. proximus* larvae but basic trends persist and are useful in distinguishing the larvae. The importance of these pigment patterns is stressed by Russell (1976) for the entire family Gadidae. He feels many of the early larvae can be identified exclusively by specific pigment patterns. We follow his terminology by referring to the postanal pigment as bars according to their position, anterior and posterior. Russell's use of the term "bar" can be confusing, however, when referring to specific areas within a bar. We define bar as: anterior and posterior pigment area each composed of a dorsal and ventral stripe. Descriptions of pigment patterns for *M. proximus* are based primarily on 49 (2.7-31.0 mm SL) recently preserved (<2 yr) specimens in which fading was minimal.

Head Region

Pigment on the head of the smallest larvae (2.7-3.6 mm SL) is limited to a spot posterior to the pigmented eye and some melanophores on the lower jaw (Figure 1A). By 4.0 mm SL, 6 or 7 melanophores appear on the nape, 5 or 6 on the lower jaw, and a few internal as well as external melanophores on the forebrain. By 5.0 mm SL, added pigment occurs between the eyes, on both jaws and at the jaw angle, and internally, posterior to the eye (Figure 1B). Snout pigment appears at 8.0 mm SL (Figure 1C), and by 10.0 mm SL, pigment is added over the dorsal region of the head (Figure 1E). Pigment is added to these areas with

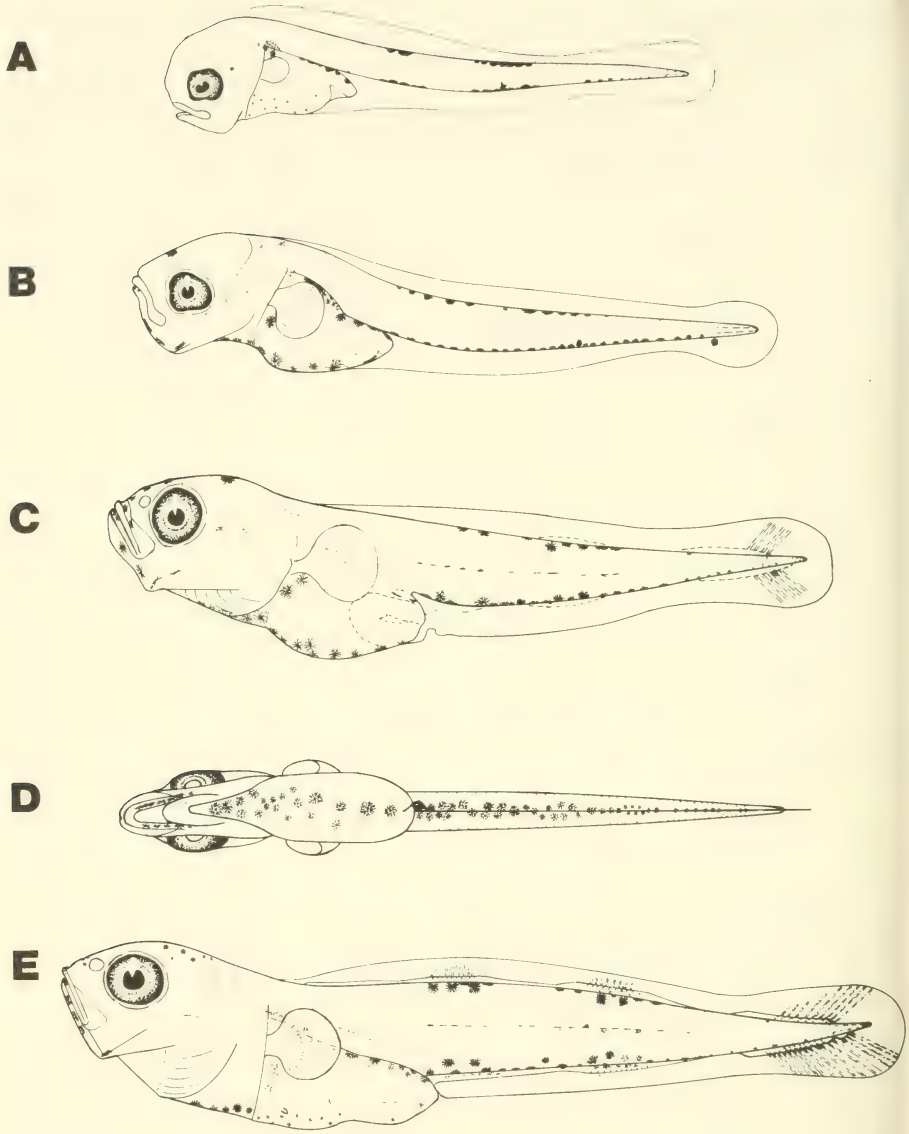


FIGURE 1.—Larval stages of *Microgadus proximus*: A. 3.6 mm SL; B. 5.7 mm SL; C. 8.4 mm SL; D. 8.4 mm SL (ventral view); E. 10.7 mm SL.

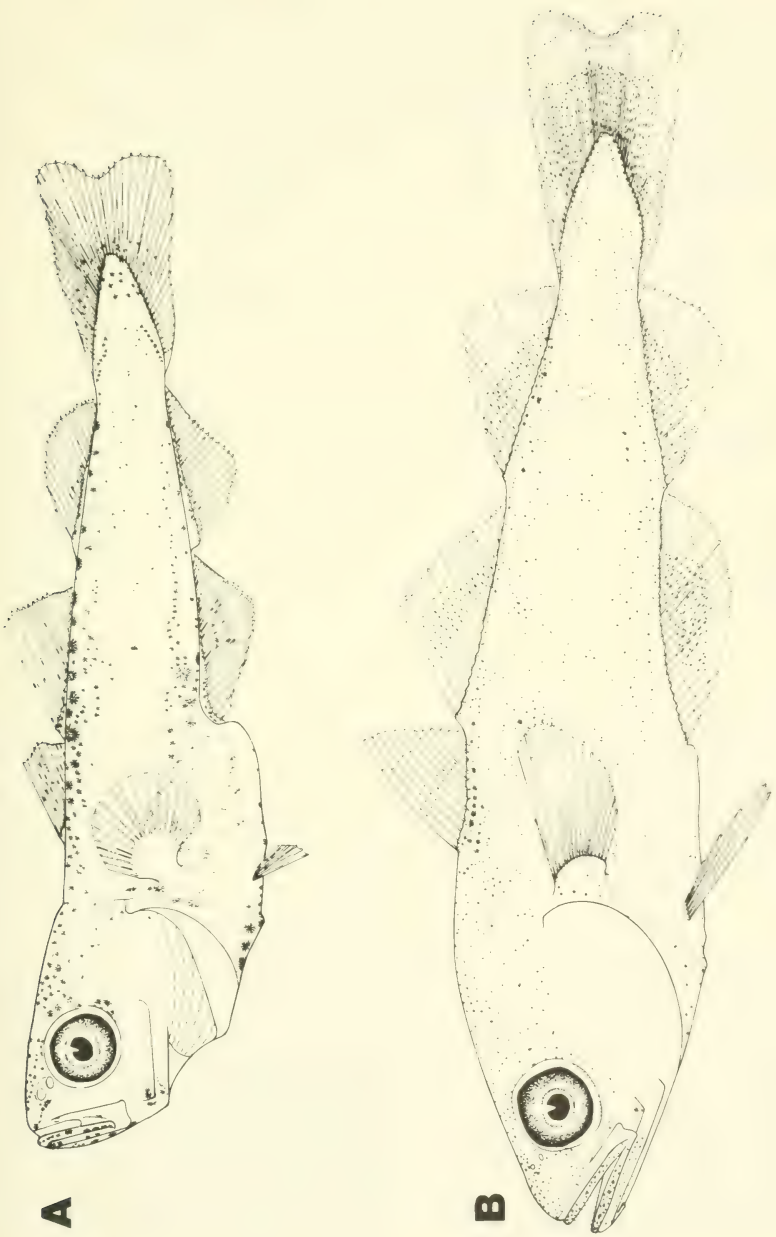


FIGURE 2.—*Microgadus proximus*: A, larva, 16.0 mm SL; B, early juvenile, 27.0 mm SL.

TABLE 1.—Summary of adult meristic counts for *Microgadus proximus*, *Theragra chalcogramma*, and *Gadus macrocephalus*. Data for *T. chalcogramma* is after Wilimovsky et al. (1967)[1] except where noted.

Species	Fin rays					Vertebrae		
	First dorsal	Second dorsal	Third dorsal	First anal	Second anal	Total	Precaudal	Caudal
M. proximus								
Sample size	37	38	39	38	38	38	38	38
Mean	12.8	18.8	20.7	25.2	22.9	55.7	19.3	36.4
Range	9-15	16-21	17-24	22-28	20-28	54-58	17-20	34-38
T. chalcogramma:								
Sample size	242	229	235	237	237	98	[2]49	[2]49
Mean	11.7	14.6	17.7	18.9	18.8	49.8	18.7	32.6
Range	10-14	12-18	15-21	16-22	16-23	48-52	18-20	31-34
G. macrocephalus:								
Sample size	40	41	42	42	41	40	40	40
Mean	12.4	15.6	15.4	19.7	17.2	53.2	19.9	33.3
Range	10-15	11-22	10-20	17-27	12-25	49-56	18-21	31-35

[1]From Wilimovsky, N. J., A. Peden, and L. Peppar. 1967. Systematics of six demersal fishes of the North Pacific Ocean. Fish. Res. Board Can., Tech. Rep. 34, 95 p.
[2]From this study.

TABLE 2.—Distribution of caudal rays on the superior hypural element in *Microgadus proximus*, *Theragra chalcogramma*, and *Gadus macrocephalus* (Walters[1] and this study).

Species	No. of specimens	Percentage of caudal rays on superior hypural			
		3	4	5	6
M. proximus	1,335	0.0	8.0	92.0	<0.1
T. chalcogramma	241	0.0	99.0	1.0	0.0
G. macrocephalus	87	0.3	97.0	0.0	0.0

[1]G. E. Walters, College of Fisheries, University of Washington, Seattle, WA 98115, pers. commun. January 1979.

development, and by 16.0 mm SL it becomes more concentrated on the jaws, jaw angle, snout, between the eyes, and over the head extending to the nape (Figure 2A). Several melanophores appear ventrally along the median cartilage between the dentaries and urohyal. With transformation (completion of fin development) at 22.0-28.0 mm SL, small and densely concentrated melanophores are added to the jaws and dorsal head (Figure 2B). The opercular area is unpigmented.

Gut Region

Melanophores line the dorsal surface of the gut cavity in the smallest larva (2.7 mm SL), and several spots are on the ventral abdominal surface anteriorly. The isthmus is pigmented by 4.0 mm SL. Melanophores increase in number on the dorsal and ventral gut surface with development. Melanophores are added laterally, occurring first anteriorly near the base of the pectoral fin at 5.0 mm SL (Figure 1B). The melanophores on the ventral surface of the gut extend more posteriorly, forming a rough line nearly to the anus by 8.0 mm SL (Figure 1C, D). Gut pigmentation changes little through transformation, except for additional melanophores on the lateral surface (Figure 2A). In early juveniles, the lateral pigment is more internal than external and the overlying skin is unpigmented (Figure 2B). Along the ventral surface of the gut is a single row of small melanophores. The base of the pectoral fin is pigmented.

Postanal Region

Pigment in the postanal region is an important diagnostic character for *M. proximus* larvae. The smallest larvae (2.7-3.6 mm SL) have two pigment bars, anterior and posterior. The stripes within the pigment bars are double rows of melanophores with pigment on both sides of the body along the dorsal and ventral midline. At first, the dorsal stripes consist of only 1 or 2 melanophores on each side, but increase to 2 or 3 anteriorly and 6-8 posteriorly by 3.6 mm SL (Figure 1A). The ventral stripes on each side have 4 or 5 spots anteriorly and 7 or 8 spots posteriorly by 3.6 mm SL (Figure 1A). At 3.6 mm SL the anterior bar is located at 42-50% SL (myomeres 16-22) and the posterior bar is at 59-72% SL (myomeres 29-37). With development, melanophores are added along the ventral stripes between the bars, becoming continuous with them by 5.7 mm SL (Figure 1B). The two dorsal stripes remain separate until 15.0 mm SL, although occasionally a few melanophores may be seen between them. Pigment is added along the body midline, externally at 7.5 mm SL and internally at 9.5 mm SL (Figure 1C, E). Postanal pigmentation changes are minimal for larvae between 10.0 and 14.0 mm SL, except for the addi-

tion of some spots laterally and in the dorsal and anal fin folds. By 15.0-16.0 mm SL, additional melanophores occur along the dorsolateral and ventrolateral surface, but those in the bars remain enlarged and distinctive (Figure 2A). After transformation, the larval pigment bars are no longer visible and the entire lateral area is pigmented, as are the dorsal and anal fins (Figure 2B).

Posterior to the second pigment bar, melanophores occur in the caudal region along the ventral body margin in the smallest larvae, connect with the ventral stripes by 5.7 mm SL (Figure 1B), and extend to the notochord tip by 6.2 mm SL. Caudal melanophores are smaller and less dendritic than those in the bars and appear as a single ventral midline row (Figure 1D). Several melanophores are added on the dorsal body margin posterior to the second pigment bar by 10.0 mm SL and, eventually, to the caudal fin fold ventrally and posteriorly by 15.0 mm SL. By 16.0 mm SL the dorsal and ventral midlines are distinctively lined with melanophores, and the lateral midline pigment, both internal and external, extends to the tail tip (Figure 2A). The proximal portion of the caudal fin is pigmented. After transformation pigment covers most of the fin (Figure 2B).

Morphology (Tables 3, 4)

Larvae of *M. proximus* are moderately elongate with the greatest body depth, about 19% SL, occurring at or near the pectoral fin base. The body tapers slightly toward the anus and then narrows abruptly posterior to the anus. The gut is only moderately long. The distance from snout to anus ranges from 41% to 48% SL in larvae and declines to 45% SL in juveniles. In our smallest yolk-sac larva (2.7 mm SL), the vent opens laterally to the right near the ventral fin fold and does not become vertical until the larvae reach about 7.5-8.5 mm SL. This lateral position of the anus in small gadid larvae was reported by Marak (1967) and Russell (1976). All yolk is absorbed by 3.0 mm SL. Notochord flexion is protracted, beginning at about 8-10 mm SL and ending at about 15 mm SL. Transformation begins at about 22 mm SL and is completed at about 27-28 mm SL. The largest pelagic specimen collected was 46.6 mm SL.

Head length as a proportion of standard length increases from 22% SL in preflexion larvae to 32% SL in transforming specimens. It declines to 30% SL in pelagic juveniles. Eye diameter as a proportion of head length decreases from 35% HL in preflexion larvae to 25% HL in pelagic juveniles, whereas snout length/head length increases from 18% HL to 29% HL. Upper jaw length/head length and body depth at pectoral fin base/standard length remain relatively constant, increasing only slightly from preflexion larvae to the pelagic juvenile stage. Depth at anus/standard length increases from 11% SL in preflexion larvae to 19% SL in juveniles.

The distance from the snout to the origin of the first dorsal fin as a proportion of standard length decreases slightly during development while the distance from the snout to the second dorsal fin/standard length remains nearly constant. The length from the snout to the origin of the third dorsal fin/standard length increases slightly during development.

Distances from the snout to the origin of the first anal fin/standard length decreases slightly from 47% SL in larvae undergoing notochord flexion to 45% SL in pelagic juveniles, whereas the snout to second anal fin distance/standard length increases slightly from 63% SL in larvae undergoing notochord flexion to 68% SL in pelagic juveniles.

Meristic Structures (Tables 5, 6; Figure 3)

Considerable variation occurs in the development of meristic structures as the size at which bones ossify varies from specimen to specimen (Table 5). The following discussion approximately parallels the sequence of development of meristic characters in *M. proximus*. Terminology of bones follows Ahlstrom and Counts (1955) and Ahlstrom.[7]

Head and Axial Skeleton

Branchiostegals can be discerned in some specimens as small as 3.9 mm SL. Ossification begins in some larvae at 8.1 mm SL, but the full complement of seven branchiostegals is not consistently ossified until the larvae are about 19 mm SL. The sequence of ossification of branchiostegals is from upper to lower.

Teeth begin ossifying on the dentary in 11.9 mm SL larvae (Table 6). Initially, the number of teeth

[7]E. H. Ahlstrom, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla, CA 92038, pers. commun. July 1979. (Deceased.)

TABLE 3.—Morphometric measurements, in millimeters, of larvae and juveniles of *Microgadus proximus*. Specimens between dashed lines are undergoing notochord flexion.

Standard length	Head length	Eye diameter	Snout length	Upper jaw length	Depth at pectoral	Depth at anus	Snout to anus	Snout to first dorsal	Snout to second dorsal	Snout to third dorsal	Snout to first anal	Snout to second anal
2.7	0.6	0.2	0.1		0.5	0.3	1.0					
2.9	0.6	0.2	0.1		0.5	0.3	1.1					
3.4	0.7	0.3	0.1		0.4	0.3	1.4					
3.8	0.8	0.3	0.1		0.5	0.4	1.4					
4.1	0.8	0.3	0.1		0.6	0.4	1.7					
4.2	0.7	0.3	0.2	0.5	0.9	0.5	1.5					
4.5	1.2	0.3	0.1	0.3	1.1	0.5	1.9					
4.7	0.9	0.4	0.1	0.3	0.8	0.5	2.0					
5.1	1.2	0.4	0.2		0.9	0.6	2.3					
5.4	1.0	0.4	0.1		0.9	0.5	2.0					
5.5	1.2	0.4	0.2	0.3	1.0	0.5	2.4					
5.9	1.5	0.5	0.2	0.4	1.0	0.6	2.6					
6.1	1.5	0.5	0.3	0.4	1.1	0.7	2.4					
6.6	1.6	0.5	0.3	0.6	1.1	0.7	2.9					
6.9	1.4	0.5	0.4	0.6	1.2	0.8	2.6					
7.1	1.7	0.6	0.4	0.7	1.3	0.9	3.3					
7.3	1.8	0.5	0.4	0.7	1.3	0.9	3.1					
7.5	1.6	0.5	0.4	0.6	1.2	0.8	3.3					
7.9	1.7	0.6	0.4	0.6	1.3	0.9	3.4					
8.1	2.0	0.7	0.5	0.7	1.6	1.2	3.6					
8.3	2.1	0.7	0.6	0.9	1.6	1.2	3.6					
8.7	2.0	0.7	0.4	0.9	1.6	1.3	4.0					
8.9	2.3	0.7	0.6	0.8	1.6	1.3	4.1					
9.0	2.2	0.7	0.6	1.0	1.6	1.2	4.0					
9.2	2.2	0.7	0.6	1.0	1.7	1.2	4.0					
9.3	2.3	0.7	0.6	1.0	1.9	1.5	4.1	3.3	4.2	6.0		
9.6	2.2	0.7	0.6	0.9	1.8	1.4	4.4					
9.7	2.5	0.7	0.7	1.0	1.8	1.5	4.5					
10.1	3.0	0.8	0.9	1.2	2.1	1.9	4.8	3.6	4.8	6.7	4.9	6.7
10.2	2.2	0.8	0.6	1.0	1.8	1.4	4.4					
10.5	2.8	0.9	0.7	1.2	2.1	1.7	4.8	3.6	4.9		4.9	
10.8	2.9	0.9	0.7	1.2	2.1	1.7	4.6	3.7	4.9		4.7	
11.4	2.9	0.9	0.7	1.3	2.1	1.9	5.2	4.1	5.1		5.3	
11.7	2.8	0.9	0.8	1.2	2.1	1.9	5.1	3.9	5.2	7.4	5.2	
12.0	3.0	1.0	0.8	1.2	2.3	2.1	5.3	3.9	5.3	7.8	5.3	
12.5	3.4	1.0	0.8	1.2	2.5	2.2	5.8	4.5	6.0		6.0	
12.7	3.5	1.2	0.9	1.4	2.6	2.2	6.0	4.4	6.0	8.4	6.0	8.6
12.9	3.5	1.2	0.9	1.4	2.6	2.6	6.3	4.7	6.4	8.8	6.5	8.8
13.5	3.5	1.1	1.0	1.4	2.6	2.4	6.3	4.7	6.2	8.6	6.4	9.1
13.7	3.8	1.2	1.1	1.4	2.6	2.5	6.6	4.9	6.4	9.2	6.6	9.8
14.0	3.8	1.1	1.0	1.7	2.8	2.8	6.5	4.7	6.2	9.0	6.5	9.3
14.2	4.0	1.2	1.0	1.5	2.8	2.5	6.7	5.0	6.7	9.2	6.7	9.3
14.5	4.3	1.3	1.3	1.7	3.0	2.7	7.2	5.3	7.0	9.7	7.2	9.8
14.7	4.5	1.3	1.3	1.7	3.0	2.7	7.3	5.7	7.3	10.5	7.5	10.2
15.2	4.5	1.3	1.2	1.7	3.0	2.7	7.2	5.2	6.8	10.0	7.2	10.0
15.3	4.5	1.3	1.2	1.8	3.3	3.0	7.5	5.7	7.3	10.8	7.5	10.5
15.5	4.3	1.3	1.3	1.7	3.0	2.8	7.3	5.7	7.5	10.2	7.5	10.2
16.2	5.0	1.4	1.4	1.8	3.5	3.3	7.8	5.8	7.8	10.7	8.0	9.2
16.5	4.7	1.3	1.3	1.7	3.5	3.2	8.0	5.8	7.7	11.0	8.2	10.8
17.0	4.8	1.4	1.4	1.8	3.4	2.7	8.5	6.2	8.0	11.5	8.7	11.3
18.3	5.3	1.5	1.7	2.0	3.8	3.3	8.8	6.7	8.8	12.3	9.0	12.5
19.0	5.5	1.5	1.7	2.0	3.5	3.5	9.3	6.5	9.5	12.8	9.5	12.7
20.0	5.7	1.6	1.7	2.2	4.2	3.7	9.3	7.2	9.5	13.6	9.5	13.2
21.0	6.2	1.7	1.8	2.3	4.3	4.2	10.0	7.5	10.3	14.7	10.0	14.7
[1]22.1	6.1	1.8	1.7	2.7	4.7	4.3	10.5	7.8	10.8	15.3	10.5	14.8
[1]23.5	6.8	1.9	2.0	2.7	4.8	4.5	10.6	8.2	10.8	16.0	10.8	16.2
[1]24.0	8.2	1.9	2.0	2.8	5.2	4.7	11.3	8.5	11.5	16.2	11.5	16.3
[1]25.2	7.8	2.1	2.3	3.0	5.5	5.2	11.8	8.8	12.2	17.5	12.0	17.5
[1]26.3	9.5	2.2	2.5	3.2	5.5	5.5	12.5	9.2	12.2	18.0	12.5	18.2
[2]27.3	8.2	2.2	2.5	3.3	5.7	5.3	13.5	9.5	12.9	18.3	13.7	20.0
[2]28.0	8.7	2.3	2.5	3.5	6.0	5.7	14.3	9.7	13.2	19.7	14.8	20.6
[2]29.3	9.2	2.3	2.7	3.7	6.3	5.7	14.2	10.3	13.8	20.5	14.2	20.3
[2]31.3	9.5	2.5	2.8	3.8	6.3	5.7	14.2	11.2	14.7	21.7	14.3	20.8
[2]32.1	9.7	2.5	2.8	3.7	6.5	5.8	14.2	11.2	14.7	21.3	14.5	22.0
[2]34.3	10.8	2.5	2.8	4.0	7.5	7.2	15.3	11.7	16.0	22.8	15.8	23.3
[2]36.7	10.8	2.7	3.0	4.5	7.7	7.3	15.2	11.7	16.8	24.6	15.7	24.6
[2]38.0	10.8	3.0	3.2	4.5	7.8	7.5	16.5	12.8	17.5	25.5	16.5	25.8
[2]38.2	11.0	2.7	3.5	4.5	7.8	7.2	15.5	13.0	17.8	25.7	16.2	25.8
[2]40.1	11.7	2.8	3.5	4.7	7.9	7.2	16.7	12.8	18.0	26.0	17.0	26.3
[2]41.1	11.2	2.9	3.5	3.3	8.2	7.2	17.3	13.3	17.8	25.8	17.3	24.0
[2]41.3	12.5	3.0	3.8	5.0	8.3	8.2	18.3	14.0	19.0	27.8	18.0	27.3
[2]46.6	14.0	3.3	4.0	5.8	9.7	9.5	20.0	15.0	21.0	31.5	20.2	32.1

[1]Transforming.
[2]Pelagic juvenile.

TABLE 4.—Body proportions of larvae and juveniles of *Microgadus proximus*. Values given for each body proportion are expressed as percentage of standard length (SL) or head length (HL): mean, standard deviation, and range.

Body proportion	Preflexion	Flexion	Postflexion	Transforming	Pelagic juvenile
Sample size	[1]19	25	10	5	13
Standard length (mm)	5.3±1.6 (3-8)	11.2±2.1 (8-15)	17.4±2.1(15-21)	24.2±1.6(22-26)	35.7±5.9(27-47)
Snout to anus length/SL	41.2±3.3 (36-47)	45.9±2.0(43-50)	48.1±1.0(47-50)	46.8±1.0(45-48)	44.6±3.3(41-51)
Head length/SL	21.9±2.6 (17-27)	26.0±2.2(22-31)	29.0±0.9(28-31)	31.6±3.6(28-36)	29.9±1.2(27-32)
Eye diameter/HL	35.1±5.0 (25-44)	31.6±2.3(27-36)	28.4±0.9(27-30)	26.1±2.8(23-30)	25.3±1.4(23-28)
Snout length/HL	17.8±7.0 (5-29)	26.6±2.3(20-30)	29.0±1.8(27-32)	27.5±2.2(24-30)	29.4±1.5(26-32)
Upper jaw length/HL	36.8±12.7(25-71)	40.9±3.4(35-46)	37.7±1.4(36-40)	38.1±4.4(34-44)	39.3±3.2(30-42)
Body depth at pectoral fin base/SL	17.3±2.7 (12-24)	19.3±1.0(18-21)	20.4±1.0(18-22)	21.2±0.6(20-22)	20.7±0.7(20-22)
Depth at anus/SL	10.8±1.1 (9-13)	16.5±2.0(13-20)	18.6±1.3(16-20)	20.0±0.7(19-21)	19.3±1.1(18-21)
Snout to first dorsal fin SL		35.2±1.5(33-39)	35.8±1.0(34-37)	35.1±0.2 (35)	33.8±1.3(31-36)
Snout to second dorsal fin SL		46.6±1.8(44-50)	47.7±1.4(45-50)	47.5±1.3(46-49)	46.1±1.1(43-47)
Snout to third dorsal fin SL		66.0±2.3(63-71)	67.5±1.7(66-71)	68.5±0.8(68-69)	67.2±2.0(63-70)
Snout to first anal fin/SL		47.3±2.2(44-51)	48.9±1.2(47-51)	47.3±0.7(46-48)	45.3±3.4(42-53)
Snout to second anal fin SL		62.5±1.6(19-72)	66.0±3.6(57-70)	68.5±1.0(67-69)	67.7±3.7(58-74)

[1]Sample size is 12 for upper jaw length.
[2]Sample size is 16 each for distances from snout to first dorsal fin and snout to second dorsal fin; 12 for distance from snout to third dorsal fin; 15 for distance from snout to first anal fin; and 9 for distance from snout to second anal fin.

on the dentary exceeds the number on the premaxilla, but this is reversed at about 23 mm SL with the difference increasing with growth. A similar change in number and location of teeth was reported to occur on the Pacific whiting, *Merluccius productus* (Ahlstrom and Counts 1955).

In larval and transforming specimens (11.9-22.3 mm SL), teeth are irregularly spaced and clustered in groups. Some are caninelike and others are recurved. As the larvae grow, the teeth become more closely spaced as the numbers of teeth increase and approach biserialization in 34.3 mm SL juveniles, similar to that described for Pacific whiting (Ahlstrom and Counts 1955).

Gill rakers begin ossifying at 9.6 mm SL and all (3 + 20 = 23) gill rakers are ossified in a 24.3 mm SL larva.

Neural spines in the abdominal region begin to ossify at about 8.7 mm SL and all are ossified by 11 or 12 mm SL. Ossification generally proceeds posteriorly. Neural spines of the caudal region also begin ossifying at about 8.7 mm SL but ossification is not complete until specimens are 17 mm SL. The neural and haemal spines of the third to sixth vertebrae preceding the postural centrum begin to accept alizarin stain before other neural spines in the caudal region. Haemal spines ossify in a sequence similar to neural abdominal spines; all spines are ossified by 17 mm SL. The last neural and haemal spines to ossify are those associated with the terminal preural vertebrae. These spines are broadly flattened and ossify simultaneously with other bones of the caudal complex, as discussed later (Figure 3).

Vertebral centra in both the abdominal and caudal regions begin to ossify at about 8.7 mm SL and ossification is completed by 11 mm SL and about 19 mm SL. Ossification proceeds from anterior to posterior.

Fins

Median and paired fins showed some variation in development, with fin rays first forming at different body lengths in individual specimens (Table 5). Fin formation occurs in the sequence: larval pectoral fins; caudal fin; first anal fin; second anal fin; third, second, and first dorsal fins (nearly simultaneously); pelvic fins; and pectoral fins with rays.

The pterygiophores supporting anal and dorsal fin rays begin ossifying at 23.4 mm SL and ossification is complete by 31.1 mm SL. Too few specimens were available to follow the sequence of ossification.

Larval pectoral fins are present in our smallest specimen (2.7 mm SL). They consist of a fleshy base and an undifferentiated membrane. They persist until rays begin differentiating late in the larval period.

The caudal fin of *M. proximus* is associated with a complex of 16 centra (2 ural and 14 preural centra), 14 neural and haemal spines, 2 epurals, 1 superior hypural (HY 4-6), and 2 inferior hypurals (HY 2-3, HY 1) (Figure 3).

Caudal rays total 49-56, of which 22-25 are dorsal in origin, 22-26 are ventral in origin, and five are normally supported by the superior hypural. Principal caudal rays number 32-33; of these, 12 or 13 are dorsal in origin and 13 or 14 are ventral in origin. One each is attached to the two epurals, five are carried on the superior hypural, two on hypural 2-3, and one on hypural 1.

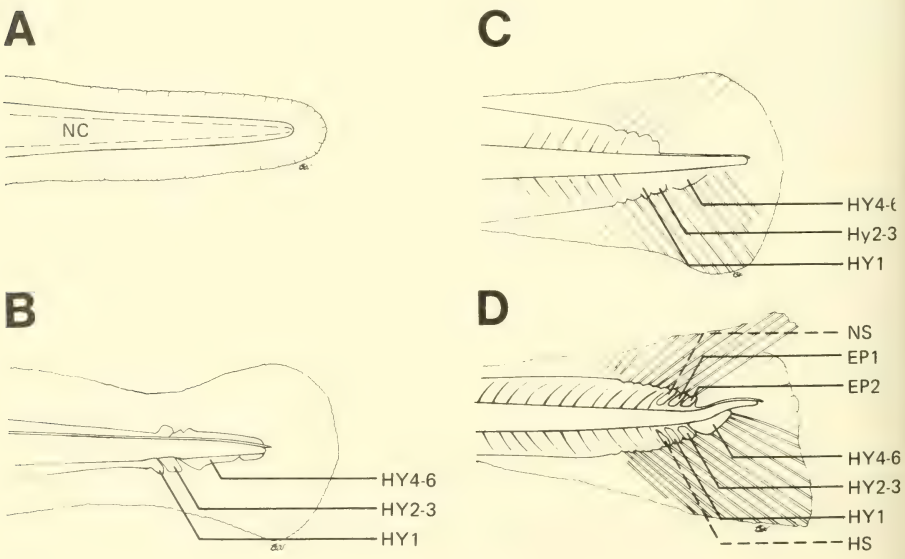
As with the Pacific whiting (Ahlstrom

and Counts 1955), some of the anterior caudal rays, both dorsally and ventrally, articulate with unmodified neural and haemal spines; other rays lie between the spines with no basal supports (Figure 3).

A symmetrical fin fold surrounds the tip of the notochord in specimens 3.1-5.5 mm SL (Figure 3). In 7.5 mm SL larvae, mesenchymal thickenings occur dorsal and ventral to the notochord. By 7.8 mm SL, the ventral thickening is differentiated into three cartilaginous plates constituting hypurals 1, 2, and 3 anteriorly, and hypurals 4-6 posteriorly (Figure 3B). In 9.5 mm SL specimens fin rays are considerably increased in number (Figure 3C). In 10.5 mm SL specimens the urostyle begins to flex, and the unossified hypurals 1, 2-3, and 4-6, as well as epurals 1 and 2 are differentiated (Figure 3D). Ossification proceeds rapidly during notochord flexion from anterior to posterior regions of the caudal complex. By 11.9 mm SL (Figure 3E), all preural centra are ossified, and all hypurals and both epurals have begun ossifying. Caudal fin rays have begun ossifying, beginning ventrally in the region of the inferior hypurals.

By 15.0 mm SL, all centra except the postural centrum are ossified; the hypurals and epurals are incompletely ossified (Figure 3F). Rays continue ossifying, proceeding posteriorly on the ventral margin and on the superior hypural and progressing anteriorly from epural number 2. By 19.4 mm SL all caudal rays posterior to preural centrum 12 are ossified. By 25.0 mm, the caudal fin is completely ossified (Figure 3G) and resembles in all details that of a 41.1 mm SL juvenile (Figure 3H).

We were unable to detect fusion of hypurals in the caudal fin of *M. proximus* during ontogeny. In the smallest larvae in which we could detect development of hypural elements (7.8-8.1 mm SL), only three hypurals could be observed. We believe, however, that these hypurals represent 1) an anterior, inferior hypural 1 (parhypural); 2) an inferior hypural representing a fusion of hypurals 2 and 3; and 3) a superior hypural representing a fusion of hypurals 4-6. This reasoning is predicated on 1) it is generally accepted that the evolutionary trend in fishes is toward a reduction in the number of hypurals, presumably by fusion of the constituent elements (Gosline 1961; Rosen and Patterson 1969; Marshall and Cohen 1973); 2) members of the family Moridae, generally considered a more primitive family than Gadidae (Svetovidov 1948; Greenwood et al. 1966; Rosen and Patterson 1969), possess three inferior and



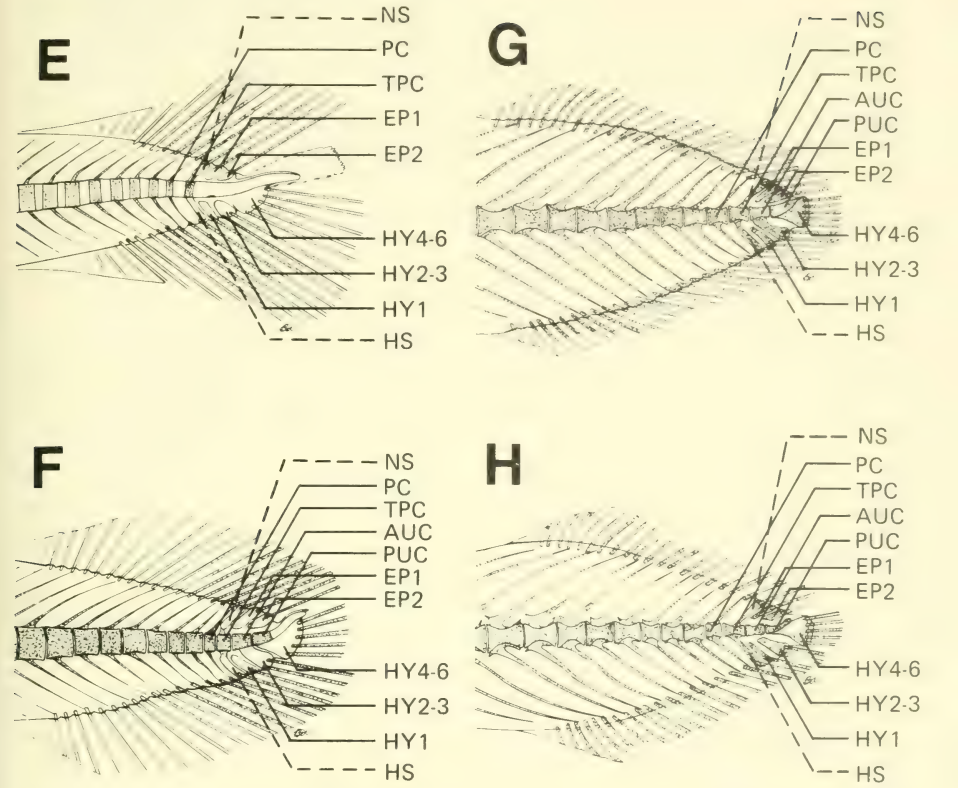


FIGURE 3.—Development of the caudal fin of *Microgadus proximus*: A. 5.2 mm SL; B. 7.8 mm SL; C. 9.5 mm SL; D. 10.5 mm SL; E. 11.9 mm SL; F.15.8 mm SL; G. 25.0 mm SL; H. 41.1 mm SL. AUC = anterior ural centrum; EP = epural; HS = haemal spine; HY = hypural; NC = notocord; NS = neural spine; PC = preural centrum; PUC = postural centrum; TPC = terminal preural centrum. Ossified elements are stippled.

three superior hypurals (Fitch and Barker 1972); and 3) presumably more advanced families of fishes in the same evolutionary line as gadids (e.g., order Batrachoidiformes) have two hypurals, apparently representing fusion of component parts (Rosen and Patterson 1969).

Barrington (1937), who figured and described the development of the caudal fin in *G. morhua*, provides the only other description of caudal development in gadids. His illustrations also depict only three hypural elements. Barrington, however, considered it unlikely that fusion of hypural bones could occur without some evidence of compound origin remaining in the fused bones. Our terminology of the caudal fin bones differs from that used by Barrington (1937) for *G. morhua*. We consider his ventral radial as hypural 1 and his dorsal radials 1 and 2 to be epurals 1 and 2.

Also we found no evidence of a uroneural in the development of the caudal fin of *M. proximus*. Rosen and Patterson (1969) consider the presence of one uroneural as a characteristic of the Gadiformes.

An anlage of the first anal fin is evident by 8.7 mm SL and the base of the second anal fin is present at 9.3 mm SL. Rays in the first anal fin begin ossifying at about 11.9 mm SL and in the second anal fin at 12.7 mm SL. Ossification is

TABLE 5.—Meristic counts from larval and juvenile *Microgadus proximus*. Values given are means. Specimens between dashed lines are undergoing notochord flexion

Length interval (mm SL)	Sample size	Dorsal fin rays			Anal fin rays		Pectoral fin rays	Pelvic fin rays	Branchiostegal rays	Gill rakers			Neural spines			Haemal spines	Centra		
		First	Second	Third	First	Second				Upper	Lower	Total	Abdominal	Caudal	Total		Abdominal	Caudal	Total
3.0- 3.9	5																		
4.0- 4.9	3																		
5.0- 5.9	6																		
6.0- 6.9	9																		
7.0- 7.9	10																		
8.0- 8.9	13								1.1				3.2	2.8	6.0	2.9	2.5	2.7	5.2
9.0- 9.9	14								1.2		1.2	1.2	5.8	7.4	13.2	7.9	5.4	7.3	12.7
10.0-10.9	16								3.0		1.0	1.0	10.6	11.5	22.1	11.3	11.6	10.6	22.2
11.0-11.9	4				4.8				4.5		1.5	1.5	19.3	24.3	43.6	24.5	19.3	27.0	46.3
12.0-12.9	8		0.8	0.6	2.9	1.0			5.0		5.6	5.6	19.1	28.1	47.2	29.0	19.1	29.0	48.1
13.0-13.9	[1]4	0.8	2.5	2.8	3.0	2.3			5.8		16.5	16.5	19.3	26.5	45.8	26.0	19.2	25.8	45.0
14.0-14.9	4	1.3	3.0	1.3	7.5	2.5		2.2	6.3				19.5	35.0	54.5	34.0	19.5	33.0	52.5
15.0-15.9	[2]4	1.3	4.3	2.8	4.5		1.3	0.5	6.5		6.5	6.5	19.5	32.3	51.8	31.0	19.5	31.8	51.3
16.0-16.9	3	1.3	1.3		3.7				6.3				18.7	21.0	39.7	19.3	18.7	28.0	46.7
17.0-17.9	[3]3	5.0	9.0	10.0	18.0	13.7	7.0	4.0	7.0	0.3	16.3	16.6	19.3	35.3	54.6	35.0	19.3	37.0	56.3
18.0-18.9	3	4.3	9.7	10.3	12.0	12.7	9.3	3.0	6.7	0.3	16.7	17.0	19.0	33.7	52.7	33.7	19.0	31.3	50.3
19.0-19.9	2	5.5	13.0	8.0	18.0	14.5	6.5	2.5	7.0	0.5	16.0	16.5	19.5	33.5	53.0	32.5	19.5	35.5	55.0
20.0-20.9	1	6.0	6.0		14.0	10.0			7.0	1.0	17.0	18.0	20.0	35.0	55.0	34.0	19.0	37.0	56.0
21.0-21.9	1	7.0	11.0	13.0	17.0	12.0			7.0	1.0	16.0	17.0	19.0	35.0	54.0	34.0	19.0	36.0	55.0
22.0-22.9	2	10.5	16.5	14.5	22.5	17.0	8.5	5.5	7.0	1.0	19.0	20.0	19.0	34.5	53.5	34.5	19.0	37.0	56.0
23.0-23.9	2	11.0	20.0	20.0	26.0	22.5	18.0	6.0	7.0	2.5	19.5	22.0	19.0	34.5	53.5	34.5	19.0	36.5	55.5
24.0-24.9	1	13.0	19.0	21.0	26.0	24.0	17.0	5.0	7.0	3.0	20.0	23.0	19.0	34.0	53.0	34.0	19.0	37.0	56.0
25.0-25.9	1	12.0	19.0	15.0	24.0	16.0	3.0	5.0	7.0	3.0	19.0	22.0	19.0	36.0	55.0	36.0	19.0	38.0	57.0
26.0-26.9	1	13.0	23.0	20.0	28.0	17.0	17.0	6.0	7.0	3.0	20.0	23.0	19.0	34.0	53.0	35.0	19.0	37.0	56.0
28.0-28.9	1	12.0	21.0	21.0	28.0	24.0	19.0	6.0	7.0	3.0	19.0	22.0	17.0	34.0	51.0	34.0	17.0	37.0	54.0
29.0-29.9	1	13.0	21.0	21.0	28.0	23.0	17.0	6.0	7.0	3.0	18.0	21.0	19.0	33.0	52.0	33.0	19.0	36.0	55.0
30.0-30.9	1	13.0	20.0	22.0	26.0	24.0	18.0	6.0	7.0	4.0	24.0	28.0	20.0	33.0	53.0	33.0	20.0	36.0	56.0
31.0-31.9	1	13.0	17.0	22.0	25.0	25.0	19.0	6.0	7.0	4.0	21.0	25.0	19.0	34.0	53.0	34.0	19.0	37.0	56.0
34.0-34.9	1	12.0	20.0	22.0	25.0	23.0	19.0	6.0	7.0	4.0	22.0	26.0	18.0	34.0	52.0	34.0	18.0	37.0	55.0
38.0-38.9	2	13.5	18.0	21.0	24.0	26.0	19.5	6.0	6.5	—	—	—	19.5	33.0	52.5	33.0	19.5	36.0	55.5
41.0-41.9	1	13.0	20.0	22.0	26.0	22.0	18.0	7.0	7.0	4.0	21.0	25.0	20.0	33.0	53.0	33.0	20.0	36.0	56.0

[1]Sample size is 3 for pectoral and pelvic fins.
[2]Sample size is 2 for second anal fin.
[3]Sample size is 2 for second dorsal fin and pectoral fin.

TABLE 6.—Numbers of teeth on premaxillary and dentary bones in selected sizes of larval and juvenile *Microgadus proximus*.

Size of specimen (mm SL)	Teeth on left side	
	Premaxilla	Dentary
Larvae:		
11.9	0	1
13.2	0	6
15.0	0	6
15.8	0	6
17.2	8	10
18.0	6	8
Transforming:		
22.3	10	14
23.4	30	24
24.3	32	27
Juveniles:		
28.6	36	24
34.3	44	35
41.1	49	38

complete in the first anal fin at 23.0 mm SL and in the second anal fin at 27 or 28 mm SL. Ray development within a fin proceeds anterior to posterior.

Dorsal fins develop in a manner analogous to the anal fins and the three dorsal fins develop almost simultaneously. Dorsal fins 2 and 3 commence ossification at 12.9 mm SL, and dorsal fin 1 begins accepting stain at 13.2 mm SL. Ossification is complete in the first and second dorsal fins at 22.0 mm SL and in the third dorsal at 28.0 mm SL. Rays ossify from anterior to posterior.

Pelvic buds appear at about 8.0 mm SL. Pelvic fins begin ossifying at about 14.0 mm SL and are consistently ossified in 26.0 mm SL early juveniles. Pectoral fins initiate ossification at 15.0 mm SL and reach their full complement of 18-20 rays in 28.0 mm SL juveniles.

Scales

Scales begin developing in the anterior portion of the body near the dorsal tip of the cleithrum in 28.6 mm SL specimens. Development appears to progress along the lateral line as the juveniles grow. Scale development was not complete in our largest specimen, 41.1 mm SL.

Occurrence of *Microgadus proximus* (Figure 4)

Although a number of ichthyoplankton studies have been conducted in the northeastern Pacific Ocean, data on occurrence of *M. proximus* are limited because of past difficulties in distinguishing the larvae from other gadids. Larvae of this species may be included under the broader category of Gadidae listed in some papers (e.g., Waldron 1972; Pearcy and Meyers 1974). Some data on distribution and seasonal abundance, however, are available.

Larvae of *M. proximus* are found in coastal waters off Oregon occurring mainly within 18 km of shore with abundance peaks at about 6 and 9 km (Richardson and Pearcy 1977; Richardson[8]). A few specimens have been reported as far as 74 km offshore (Richardson footnote 8).

The larvae have been collected in the plankton off Oregon from February through August with peak abundance from March through July (Richardson footnote 8). Misitano (1977) also collected four specimens, 5-61 mm SL, from March to July in the Columbia River mouth.

Monthly length frequencies and median lengths of larvae collected in 1971 and 1972 off Oregon indicate a winter-spring spawning period (Figure 4). Small larvae, ≤5 mm SL, were collected February through June.

Larvae of *M. proximus* were collected 24 km off coastal Washington (Cruise K-72-2-III) in early June 1972, by the NWAFC[9]. This species accounted for 22.2% of the total catch of fish larvae, and specimens ranged from 5.0 to 26.0 mm SL.

COMPARATIVE NOTES ON *THERAGRA CHALCOGRAMMA* AND *GADUS MACROCEPHALUS* (Figure 5, Table 7)

In the northeastern Pacific Ocean, larvae of *M. proximus* are similar to those of *T. chalcogramma* and *G. macrocephalus* at sizes <16.0 mm SL. Identification of all three species in mixed samples is difficult with previously available literature, which describes *T. chalcogramma* and *G. macrocephalus* from the northwestern Pacific Ocean (e.g., Gorbunova 1954; Uchida et al. 1958; Mukhacheva and Zviagina 1960). We have summarized characters which are useful to distinguish each species at sizes <16.0 mm SL based on our examination of specimens of all three species (Table 7).

The most useful character to separate the smaller larvae (hatching to 10.0 mm SL) of the

[8]Richardson, S. L. 1977. Larval fishes in ocean waters off Yaquina Bay, Oregon: abundance, distribution, and seasonality January 1971 to August 1972. Oregon State Univ., Sea Grant Coll. Program Publ. ORES-T-77-003, 73 p.

[9]Data on file for Cruise K-72-2 (III), 1972. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112.

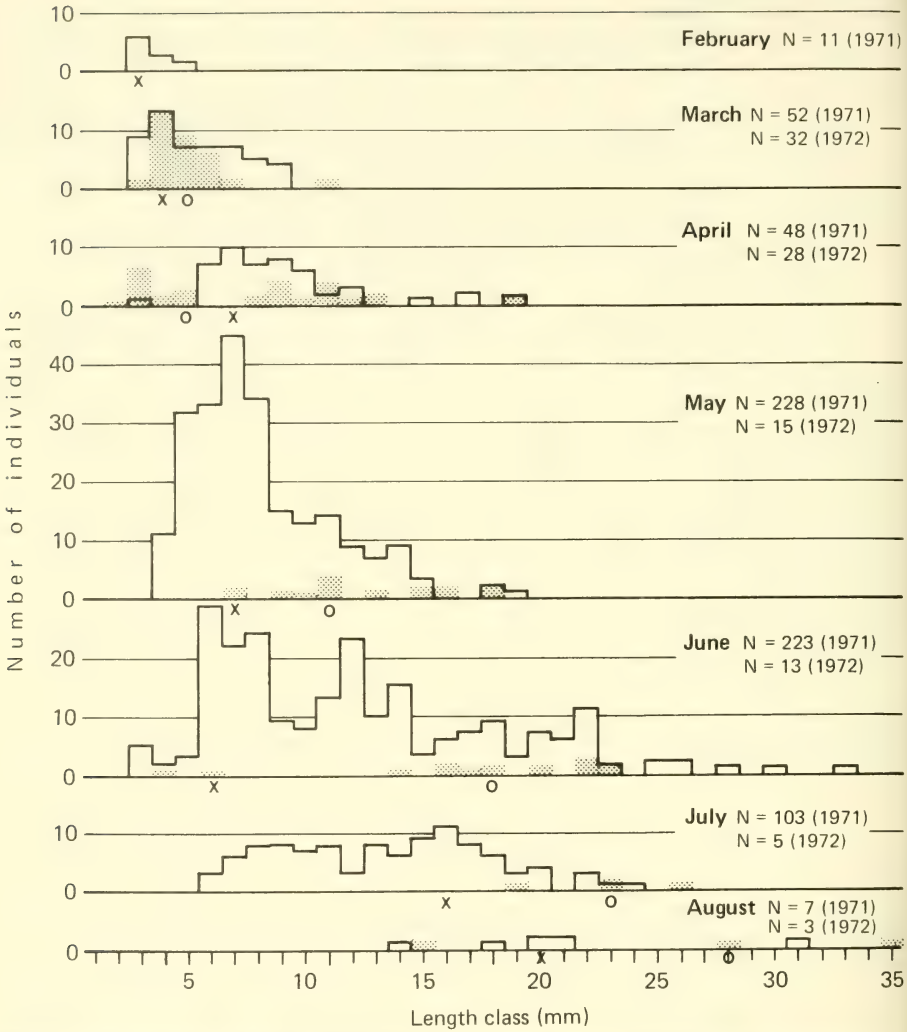


FIGURE 4.—Length-frequency histograms of *Microgadus proximus* larvae collected in 70 cm bongo nets off Oregon in 1971 (unshaded) and 1972 (shaded). X = median length class of larvae in 1971; O = median length class of larvae in 1972.

three species is the length and position of the anterior and posterior postanal pigment bars. In *M. proximus* larvae 5.0-6.0 mm SL (Figure 1B), the anterior bar begins just posterior to the anus at 41-53% SL (myomeres 14-23) and the posterior bar is at 61-74% SL (myomeres 28-39). In *T. chalcogramma* larvae of the same size range (Figure 5A), the anterior bar begins posterior to the anus at

47-55% SL (myomeres 21-26) and the posterior bar is at 69-79% SL (myomeres 36-43). The anterior bar begins posterior to the anus for similar size *G. macrocephalus* larvae (Figure 5C) at 40-57% SL (myomeres 16-26) and the posterior bar is at 59-81% SL (myomeres 26-42). Differences also exist in the number of melanophores in the stripe within a bar and associated bar length. This latter character, however, is only useful at small sizes (2.5-4.5 mm SL) because melanophores increase with development and the stripes become continuous. At 3.6 mm SL (Figure 1A), *M. proximus* larvae have on each side two dorsal and four ventral melanophores in the stripes within the small anterior bar, and seven melanophores each in the longer dorsal and ventral stripes within the posterior bar. Similar sized *T. chalcogramma* larvae (4.1 mm SL) have evenly sized stripes with five melanophores on both the dorsal and ventral stripe of the anterior bar, and five dorsal and seven ventral melanophores in each stripe of the posterior bar. *Gadus macrocephalus* larvae (4.4 mm SL) have longer stripes than the other two species, with 7 dorsal and 8 ventral melanophores on the anterior bar, and 11 dorsal and 10 ventral melanophores on the posterior bar.

With development these pigment stripes within the bars variously remain separate or become connected depending on the species. In *M. proximus* larvae the ventral stripes become continuous at 5.0-6.0 mm SL (Figure 1B) while the dorsal stripes remain separate until 13.0 mm SL. The dorsal stripes become continuous in *T. chalcogramma* larvae at 13.0 mm SL whereas the ventral stripes never connect. *Gadus macrocephalus* larvae have continuous dorsal and ventral stripes of melanophores by 5.0-6.0 mm SL (Figure 5C).

Other pigment differences may help in distinguishing species at certain size ranges. Early *G. macrocephalus* larvae (4.0-8.0 mm SL) have more head pigmentation than the other two species, particularly on the dorsal surface and in the snout area (Figure 5C). *Theragra chalcogramma* larvae (<13.0 mm SL) have much less lateral pigment on the surface of the gut than either *M. proximus* or *G. macrocephalus* larvae (Figure 5B). *Gadus macrocephalus* larvae (5.0-8.0 mm SL) have more mediolateral pigmentation between the postanal bars than the other two species in that size range (Figure 5C). Caudal pigment also differs and at sizes <10.0 mm SL can separate *M. proximus*. Only *M. proximus* larvae have a single row of ventral caudal melanophores posterior to the anal fin (Figure 1D) whereas both *T. chalcogramma* and *G. macrocephalus* larvae have isolated pigment spots (Figure 5B, D).

Also helpful in distinguishing *M. proximus* larvae from the other two species is the possession of five rays on the superior hypural compared with four rays for *T. chalcogramma* and *G. mac-*

TABLE 7.—Characters useful in separating larvae of *Microgadus proximus*, *Theragra chalcogramma*, and *Gadus macrocephalus* at specific size ranges.

Character	Size range (mm)	*Microgadus proximus*	*Theragra chalcogramma*	*Gadus macrocephalus*
Anterior pigment bar	5-6			
Percentage of SL		41-53	47-55	40-57
Located at myomeres		14-23	21-26	16-26
Posterior pigment bar	5-6			
Percentage of SL		61-74	69-79	59-81
Located at myomeres		28-39	36-43	26-42
Number of melanophores in each stripe of:				
Anterior bar	3-4			
Dorsal		2	5	7
Ventral		4	5	8
Posterior bar	3-4			
Dorsal		7	5	11
Ventral		7	7	10
Degree of stripe continuity:				
Anterior bar:				
Dorsal	5-13	Separate	Separate	Continuous
Ventral		Continuous	Separate	Continuous
Posterior bar:				
Dorsal	13-16	Separate	Continuous	Continuous
Ventral		Continuous	Separate	Continuous
Head melanophores	4-8	—	—	More on dorsal surface and snout
Melanophores on ventral surface of gut	>13	1-2 rows of spots	No spots or a few reduced spots	1-2 rows of spots
Lateral pigment on gut surface	<13	—	Much less	—
Mediolateral pigment in postanal region	5-8	—	—	More
Ventral caudal pigment	<10	Row of spots	Isolated spots	Isolated spots
Number of rays on superior hypural element	>13	5	4	4

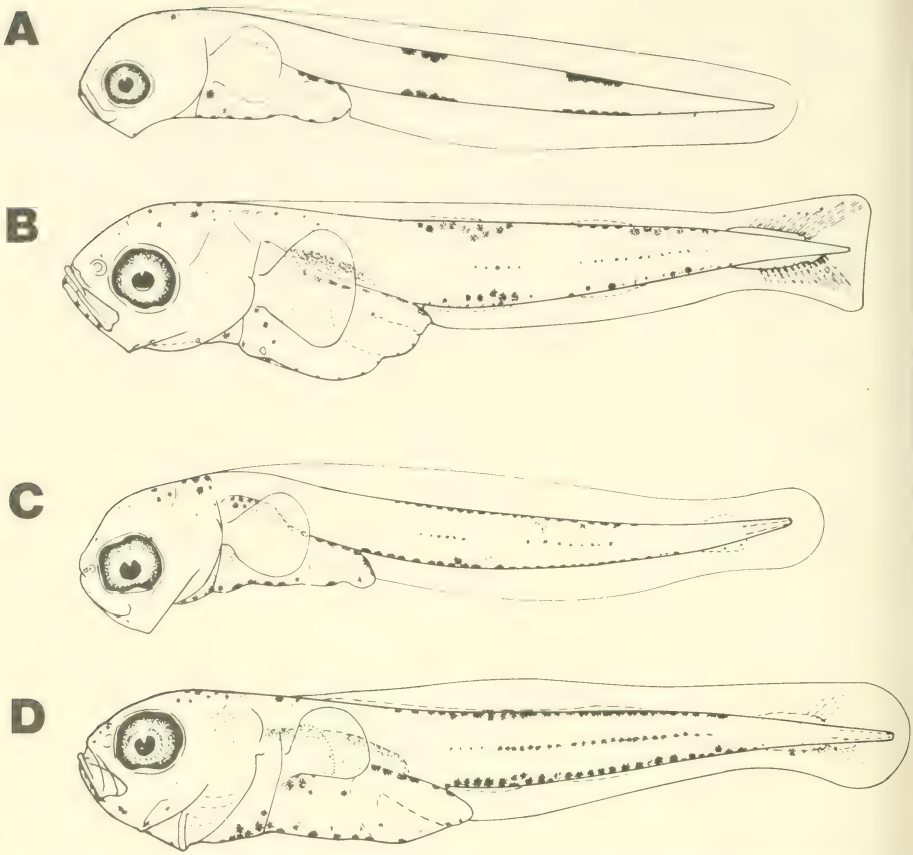


FIGURE 5.—Larvae of *Theragra chalcogramma* and *Gadus macrocephalus*: A. *T. chalcogramma*, 6.2 mm SL; B. *T. chalcogramma*, 9.8 mm SL; C. *G. macrocephalus*, 5.6 mm SL; D. *G. macrocephalus*, 8.5 mm SL.

rocephalus. This character can be useful in a size range (>13.0 mm SL) which may be troublesome when pigment patterns are no longer helpful and adult characters (e.g., barbel length, mouth and anus position, or shape of fins) are not fully developed. Larvae >20.0 mm SL may also be distinguished by a combination of meristic counts (Table 1).

ACKNOWLEDGMENTS

We thank the following at the NWAFC, NMFS, NOAA: Beverly Vinter who provided great assistance in the interpretation of distinguishing characteristics in gadid larvae and illustrated the larvae and caudal fin; Bernie Goiney and Jay Clark for technical assistance; and Arthur Kendall for helpful discussions.

April G. Maclean, formerly OSU, assembled a large portion of the *M. proximus* series and made some of the counts and measurements. Joanne L. Laroche (OSU) helped gather additional specimens from OSU collections.

Gary Walters, FRI, has a continuing interest in

gadid larvae and juveniles and provided us with unpublished data and gave other assistance.

A number of workers graciously provided us with samples of larval and juvenile gadids without which we could not have completed this work. We therefore thank: Douglas Rabin, Gary Walters, William Karp, and Bruce Miller, FRI; T. Saunders English, Department of Oceanography, University of Washington; Jay Quast and Bruce Wing, NWAFC Auke Bay Laboratory, NMFS, NOAA; James Blackburn, Alaska Department of Fish and Game (ADF&G), Kodiak; Lou Barton, ADF&G, Anchorage; and Rollin Daggett, Ecology Consultants, Inc., Fort Collins, Colo.

Norman Wilimovsky, University of British Columbia, Vancouver, loaned us radiographs of adult pollock. Elbert Ahlstrom, Southwest Fisheries Center La Jolla Laboratory, NMFS, NOAA, provided stimulating discussions on gadid osteology and on the interpretation of caudal fin development.

A draft of this manuscript benefited from reviews by Michael Fahay, Northeast Fisheries Center Sandy Hook Laboratory, NMFS, NOAA, and Arthur Kendall.

LITERATURE CITED

AHLSTROM, E. H., AND R. C. COUNTS.
1955. Eggs and larvae of the Pacific hake, *Merluccius productus*. U.S. Fish Wildl. Serv., Fish. Bull. 56:295-329.

BARRINGTON, E. J. W.
1937. The structure and development of the tail in the plaice (*Pleuronectes platessa*) and the cod (*Gadus morrhua*). Q. J. Microsc. Sci. 79:447-469.

BEARDSLEY, A. J., AND C. E. BOND.
1970 Field guide to common marine and bay fishes of Oregon. Oreg. State Univ. Agric. Exp. Stn. Bull. 607, 27 p.

BOOTH, R. A.
1967. A description of the larval stages of the tomcod, *Microgadus tomcod*, with comments on its spawning ecology. Ph.D. Thesis, Univ. Connecticut, Storrs, 53 p.

CLEMENS, W. A., AND G. V. WILBY.
1961. Fishes of the Pacific coast of Canada. 2d ed. Fish. Res. Board Can., Bull. 68, 443 p.

DINGERKUS, G., AND L. D. UHLER.
1977. Enzyme clearing of alcian blue stained whole small vertebrates for demonstration of cartilage. Stain Technol. 52:229-232.

FITCH, J. E., AND L. W. BARKER.
1972. The fish family Moridae in the eastern North Pacific with notes on morid otoliths, caudal skeleton, and the fossil record. Fish. Bull., U.S. 70:565-584.

GORBUNOVA, N. N.
1954. Razmnozhenie i razvitie mintaya, *Theragra chalcogramma* (Pallas). (The reproduction and development of the walleye pollack, *Theragra chalcogramma* (Pallas).) [In Russ.] Akad. Nauk SSSR, Tr. Inst. Okeanol. 11:132-195. (Translated by S. Pearson, 1972, 106 p.; available Northwest and Alaska Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, Wash.)

GOSLINE, W. A.
1961. The perciform caudal skeleton. Copeia 1961:265-270.

GREENWOOD, P. H., D. E. ROSEN, S. H. WEITZMAN, AND G. S. MYERS.
1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. Bull. Am. Mus. Nat. Hist. 131:339-456.

HART, J. L.
1973. Pacific fishes of Canada. Fish. Res. Board Can., Bull. 180, 740 p.

ISAACSON, P. A.
1965. Southern range extension of the tomcod, *Microgadus proximus*. Calif. Fish Game 51:58.

MARAK, R. R.
1967. Eggs and early larval stages of the offshore hake, *Merluccius albidus*. Trans. Am. Fish. Soc. 96:227-228.

MARSHALL, N. B., AND D. M. COHEN.
1973. Order Anacanthini (Gadiformes): Characters and synopsis of families. *In* D. M. Cohen (editor-in-chief), Fishes of the western North Atlantic, Part six, p. 479-495. Mem. Sears Found. Mar. Res., Yale Univ. 1.

MILLER, D. J., AND R. N. LEA.
1972. Guide to the coastal marine fishes of California. Calif. Dep. Fish Game, Fish Bull. 157, 235 p.

MISITANO, D. A.
1977. Species composition and relative abundance of larval and post-larval fishes in the Columbia River estuary, 1973. Fish. Bull., U.S. 75:218-222.

MUKHACHEVA, V. A., AND O. A. ZVIAGINA.
1960. Razvitie tikhookeanskoi treski *Gadus morhua macrocephalus* (Tilesius). (Development of the Pacific cod *Gadus morhua macrocephalus*, (Tilesius).) [In Russ.] Akad. Nauk SSSR, Tr. Inst. Okeanol. 31:145-165. (Translated by W. E. Ricker, available Fish. Mar. Serv., Pac. Biol. Stn., Nanaimo, B.C., as Fish. Res. Board Can. Transl. Ser. 393.)

PEARCY, W. G., AND S. S. MYERS.
1974. Larval fish of Yaquina Bay, Oregon: A nursery ground for marine fishes? Fish. Bull., U.S. 72:201-213.

RICHARDSON, S. L., AND W. G. PEARCY.
1977. Coastal and oceanic fish larvae in an area of upwelling off Yaquina Bay, Oregon. Fish. Bull., U.S. 75:125-145.

ROSEN, D. E., AND C. PATTERSON.
1969. The structure and relationships of the paracanthopterygian fishes. Bull. Am. Mus. Nat. Hist. 141:357-474.

RUSSELL, F. S.
1976. The eggs and planktonic stages of British marine fishes. Acad. Press, Lond., 524 p.

SCHULTZ, L. P., AND A. D. WELANDER.
1935. A review of the cods of the Northeastern Pacific with comparative notes on related species. Copeia 1935: 127-139.

SVETOVIDOV, A. N.
1948. Treskoobraznye (Gadiformes). [In Russ.] Akad. Nauk SSSR, Zool. Inst., Fauna SSSR, Ryby, t. 9, Vyp. 4, N.S. 34, 221 p. (Translated by Isr. Program Sci. Transl., 1962, 304 p.; available Natl. Tech. Inf. Serv., Springfield, Va., as OTS 63-11071.)

TANNER, Z. L.
1894. Report upon the investigations of the U.S. Fish Commission steamer *Albatross* for the year ending June

30, 1892. U.S. Comm. Fish Fish., Part 18, Rep. Comm. 1892, append. 1, 64 p.

TAYLOR, W. R.
1967. An enzyme method of clearing and staining small vertebrates. Proc. U.S. Natl. Mus. 122(3596), 17 p.

UCHIDA, K., S. IMAI, S. MITO, S. FUGITA, M. UENO, Y. SHOJIMA, T. SENTA, M. TAHUKU, AND Y. DOTU.
1958. Studies on the eggs, larvae and juveniles of Japanese fishes. [In Jpn.] Kyushu Univ., Fac. Agric., Fish. Dep., 2d Lab., Ser. 1, 85 p. (Translation of p. 26-27, 30-31, and 65 by W. G. Campen, 1961, 8 p.; available Northwest and Alaska Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, Wash.)

WALDRON, K. D.
1972. Fish larvae collected from the northeastern Pacific Ocean and Puget Sound during April and May 1967. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-663, 16 p.

WILIMOVSKY, N. J.
1964. Inshore fish fauna of the Aleutian Archipelago. Proc. Alaska Sci. Conf. 14:172-190.

YUSA, T.
1954. On the normal development of the fish, *Theragra chalcogramma* (Pallas), Alaska pollock. [In Jpn., Engl. summ.] Bull. Hokkaido Reg. Fish. Res. Lab. 10:1-15.

NOTES

PREDATION BY SHARKS ON PINNIPEDS AT THE FARALLON ISLANDS[1]

What we know about mortality in pinnipeds has largely been derived indirectly. For example, pinnipeds or parts thereof have occasionally been found in shark stomachs. Sharks have thus become known as pinniped predators (e.g., Gogan[2]), but, since few direct observations of shark/pinniped interactions exist, we do not know the extent of such predation. The present paper summarizes observations of shark/pinniped encounters at the Farallon Islands between 1970 and 1979. We relate the frequency of observed encounters to annual and seasonal changes in pinniped population, and the marine climate, and assess the effect of shark-bite injury on the reproductive performance of seals.

Methods

The South Farallon Islands, San Francisco County, Calif. (lat. 37.4° N, long. 123.0° W), lie at the inward edge of the California Current, 30 km west of the California coast. Southeast Farallon, West End, and accompanying rocks compose the South Farallones and in all are about 44 ha (Figure 1). Over 250,000 seabirds of 12 species breed there (Ainley and Lewis 1974). Pinnipeds reach a peak of 2,500 animals—three species breed and occur there year-round: harbor seal, *Phoca vitulina*, northern elephant seal, *Mirounga angustirostris*, and northern sea lion, *Eumetopias jubatus*; a fourth, California sea lion, *Zalophus californianus*, the most numerous of Farallon pinnipeds, occurs most abundantly in spring, but few breed there; and a fifth, northern fur seal, *Callorhinus ursinus*, occasionally hauls out (Pierotti et al. 1977; Ainley et al.[3]).

Since 1968, the Point Reyes Bird Observatory has maintained a year-round research station on Southeast Farallon. On a rotating but continual schedule at least two biologists, plus several volunteer workers, have operated the station. Every day, weather permitting, a census of birds and a general visual survey of inshore waters was made. Beginning in 1970 elephant seals were

[1]Contribution 169 of the Point Reyes Bird Observatory.

[2]Gogan, P. J. P. 1977. A review of the population ecology of the northern elephant seal, *Mirounga angustirostris*. Unpub. manuscr., 68 p. Natl. Mar. Mammal Lab., NMFS, NOAA, 7600 Sandpoint Way, NE., Seattle, WA 98115.

[3]Ainley, D. G., H. R. Huber, R. P. Henderson, T. J. Lewis, and S. H. Morrell. 1976. Studies of marine mammals at the Farallon Islands, California, 1975-76. Final report, Marine Mammal Commission (Contract No. MM5AC027), Wash., D.C., available Natl. Tech. Inf. Serv., Springfield, VA 22151 as PB 2-266249, 32 p.

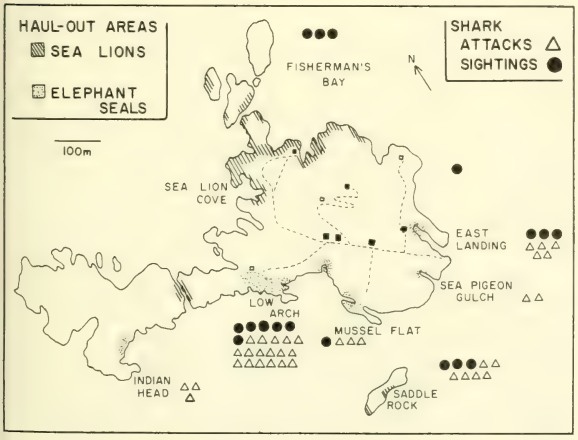


FIGURE 1.—South Farallon Islands, central California, and location of observed shark/pinniped encounters and major haul-out areas of sea lions and elephant seals.

censused weekly during most of the year and daily during the breeding season. Regular weekly censuses of other pinnipeds have been conducted since 1972, and as far back as 1970 irregular counts were made. Since we found shark activity to be seasonal (see below), we included comments on the seasonal changes in sea-surface temperature and salinity. Such information was derived from daily readings made at noon (P.s.t.).

Results

We recorded events involving sharks 58 times between 9 September 1970 and 9 February 1979. Of these, 37 were definite observations of sharks eating pinnipeds (i.e., "shark attacks") and the remainder (21) were mostly of sharks seen within 1 km of the island. In definite shark attacks, we were first (36 of 37 times) alerted to the incident by a flock of gulls (mostly the western gull, *Larus occidentalis*), hovering above a large bloody area (5 m^2) in the water. Usually we saw the shark's head and dorsal and caudal fins which offered clues to species identification and estimation of size and number. We often saw the pinniped prey as well. On five occasions only an area of bloody water and the hovering gulls were observed. These, too, were likely shark attacks on pinnipeds, but we did not include them in the 37 known attacks. Observations, from discovery of the gull flock to dissipation of blood and gulls, lasted from 3 to 15 min. If the carcass was not consumed in that time, then its disappearance was probably due to sinking. In the areas of most shark/pinniped interactions the water was 4-12 m deep.

In 20 interactions we saw the pinniped prey sufficiently well for a positive identification. Two involved sea lions, one or perhaps two involved harbor seals, and the remainder involved elephant seals. Based on size, we could tell that seven elephant seals were young individuals, about 3 yr old or less, and an eighth was an adult female. On rare occasions, we have observed sea lions with obvious, fresh shark-bite wounds. However, the location of most shark attacks in the vicinity of the elephant seal hauling out areas (Figure 1) further supports what other data indicate, that at Southeast Farallon, sharks more frequently ate elephant seals than other pinnipeds.

In 30 instances, the white shark, *Carcharodon carcharias*, was identified as the species seen preying on seals. All were at least 3 m long and most about 3.5-5 m long. In 16 of 21 nonattack observations within 1 km of the island, the shark was also identified: 14 involved white sharks and two involved the blue shark, *Prionace glauca*. How many sharks were present at any one time is not known. On at least three occasions two sharks, and once three sharks, simultaneously fed on one pinniped. On 8 January 1976, a 3 m long white shark was caught in Fisherman's Bay and 7 d later two larger white sharks were seen on the opposite side of the islands.

Sharks were more abundant or more active during the late fall and winter over the 9 yr (Figure 2). The number of attacks in December and January was perhaps artifically low (see below) because on many days during those months few if any gulls were present to alert observers. The possibility that attacks were missed was particularly likely in December 1976 and January 1977. Sharks were known to be present then because several seals hauled out with fresh shark-bite wounds and part of another was seen floating in the water. Yet no attacks were seen. The timing of greatest shark activity corresponded closely with the Davidson Current period (October-February) which, as described by Bolin and Abbott (1963), is characterized by slowly declining sea-surface temperatures and salinities and the appearance of a northward flowing countercurrent (shoreward of the south-flowing California Current). White sharks were thus present (or at least active, see below) when waters were warm but not necessarily the warmest (Figure 2). Blue sharks, on the other hand, were definitely most abundant during the warm oceanic period (July-September), when the California Current slackens, allowing warm saline oceanic waters to flow shoreward. They were observed commonly but only at 3 km or more away from the island. Few were involved in the observations reported here.

The timing of most shark attacks also corresponded closely with the late autumn peak in elephant seal numbers (Figure 2). Each year the elephant seals reached maximum numbers twice, during midspring and again during late fall (Le Boeuf et al. 1974). A third, smaller peak occurred during the winter breeding season. Only two shark attacks, both involving elephant seals, were observed during the upwelling period (March-July), when the California Current flows most strongly and temperatures reach their lowest. One of these attacks occurred during the spring peak in elephant seal numbers. During the fall, when most shark attacks were observed,

the populations of other pinniped species at the Farallones were usually near their annual low (Ainley et al. footnote 3), which indicates even further that elephant seals were the usual prey of sharks. Rather exceptional were the high numbers of California sea lions present in the fall 1978 (Huber et al.[4]). Sharks and shark incidents were seen often then but we could identify few of the pinniped prey. One incident definitely involved a sea lion but most others occurred in areas frequented by elephant seals and not by sea lions.

Several elephant seals arrived at the Farallones for the breeding season bearing shark-bite wounds, some fresh and some healed. The histories of these animals are noteworthy, particularly since their being severely wounded may have affected their reproductive performance. Twenty-four breeding attempts by females identifiable as individuals were available for analysis. In 10 attempts, females arrived with fresh wounds. In only one (10%) did she successfully rear a pup by herself, three lost their pups, three received help from other cows (i.e., they shared suckling), and three apparently did not pup. In 1977 three newly wounded cows disappeared (not even present during spring molt) after leaving the island with healed wounds. In 14 pupping attempts by known females with no wounds (but wounded in a later year) or with old, healed wounds, all but two (86%) successfully raised a pup without help. The difference is significantly different from the 10 attempts mentioned above ($t = 3.3$, $P<0.001$). Since many of the freshly wounded females were probably pupping for their first time, it could have been lack of experience that resulted in their poor record rather than being wounded. Two females, however, without wounds raised their first pups successfully but the next season, each with a fresh wound, they either allowed another cow to help in suckling or failed to pup successfully. In addition, of 11 females pupping for their first time in 1977 and not having shark-bite wounds, 7 (64%) were successful, and only 1 allowed its pup to be nursed by another female. Thus females with fresh, severe shark-bite wounds were less successful in pupping than others. Perhaps the energy and tissue-building resources needed to heal a severe wound were taken from those required in the rearing of a pup. None of the 6 females with fresh shark wounds in the 1977 breeding season was observed to copulate; among other females 99 (77%) were observed in copulation.

Two male elephant seals have also hauled out at the Farallones, bearing shark-bite wounds. One first visited in December 1972 as a subadult bull (probably about 5 yr old) and had an old shark-bite wound. He returned each season through the 1976 breeding season. Another was first seen in 1972 as a young adult (Le Boeuf et al. 1974) and was the alpha bull in the breeding hierarchy during 1972, 1973, and 1974. In 1975 he arrived for the fourth year, was initially the alpha bull, but was dethroned before the end of the breeding season. In 1976 he appeared on the island with two fresh shark wounds. Thereafter he visited the breeding colony intermittently, but was not part of the hierarchy of breeding bulls.

[4]Huber, H. R., D. G. Ainley, S. H. Morrell, R. R. LeValley and C. S. Strong. 1978. Studies of marine mammals at the Farallon Islands, California, 1977-78. Final report, Marine Mammal Commission (Contract No. MM7AC025), Wash., D.C., available Natl. Tech. Inf. Serv., Springfield, VA 22151 as PB 80-111602, 50 p.

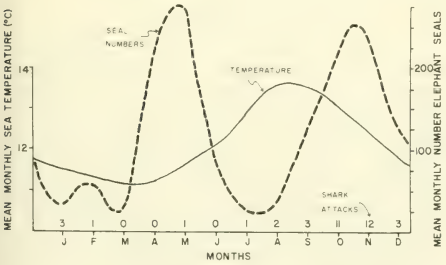


FIGURE 2.—Annual cycles in monthly mean sea-surface temperature, elephant seal numbers and number of shark/pinniped interactions in the Farallon Islands, central California, vicinity, 1970-78. Seal numbers are from Ainley et al. (text footnote 3) and Huber et al. (text footnote 4).

Discussion

It is obvious that the frequency of shark attacks on pinnipeds and other shark observations have been increasing at the South Farallon Islands (Table 1). We are convinced this is not an artifact of increasing observer awareness for a number of reasons, because a flock of 50+ gulls hovering for 10-15 min above a large, blood-red patch of water within 50 m of shore is not easy to miss, particularly from such a small island; and daily censuses have been conducted consistently since 1970.

Since the seasonal occurrence of some sharks is related to water temperatures (e.g., O'Gower

TABLE 1.—Annual data on elephant seal numbers, shark attacks, water temperatures, and frequency of attacks relative to seal numbers at the Farallon Islands, central California.

	Winter (late December-February)				Summer (late March-early July)				Fall (late August-mid-December)			
Year	A Max no. seals	B No. attacks	C Ratio A:B	Mean sea temp	A Max no. seals	B No. attacks	C Ratio A:B	Mean sea temp	A Max no. seals	B No. attacks	C Ratio A:B	Mean sea temp
1970	0	0	0	11.3	60	0	0	10.0	35	[1]1	0	15.5
1971	0	0	0	11.5	50	0	0	[2]8.8	120	0	0	16.8
1972	3	0	0	11.5	120	0	0	10.0	155	1	.01	17.0
1973	10	0	0	12.1	176	0	0	10.8	170	2	.01	14.5
1974	20	0	0	11.0	290	1	.003	8.8	300	2	.01	15.0
1975	30	[2]0	0	10.9	305	0	0	10.0	330	6	.02	13.5
1976	55	0	0	10.5	460	0	0	9.3	450	4	.01	16.0
1977	110	[2]0	0	12.7	523	0	0	10.0	507	7	.01	13.6
1978	182	4	.02	13.6	717	1	.001	12.4	609	7	.01	12.0
1979	250	[2]1	.004	11.6	776	0	0	11.2				

[1] Thought to be an attack on a sea lion.
[2] Cows arrived with fresh shark-bite wounds; in 1979 the remains of a cow, likely a shark victim, was seen floating in the water.

and Nash 1978), it was worthwhile to consider the relationship between temperature and sharks at the Farallones. As shown in Table 1, water temperature during the fall when most shark attacks and sightings occurred, compared among the years, fluctuated up and down but did not relate clearly to yearly fluctuation in shark attack frequency. The same was true for temperatures during the winter elephant seal breeding season. The year 1978 provides an instructive example of this. In the spring-summer, temperatures were unusually high. In spite of record numbers of elephant seals only one shark attack was observed, and that occurred in July, long after the seal population peak (only 24 were present; 452 sea lions, though, were present). Later in the fall, temperatures were lower than during spring but much shark activity was evident (Table 1). The only major relationship that was evident between shark attacks and water temperature was that all but one observed attack occurred when temperature generally exceeded 12° C (as summarized in Figure 2). Unfortunately, there is no published information of the seasonality of white sharks to explain this. Off Durban, South Africa, where water temperatures are higher than at the Farallones, Bass (1978) found small white sharks more abundant when temperatures dropped to the annual low (equivalent to highest Farallon temperatures), but the number of white sharks the size of those at the Farallones did not change.

The factor that best relates to the general increase in white sharks is an increase in elephant seal numbers. The fall, winter, and spring populations of elephant seals have been increasingly rapidly at the Farallones over the past several years (see Le Boeuf et al. 1974; Ainley et al. footnote 3; Table 1). The seal population during the fall, the period of most shark attacks, has increased about 3.9 fold since 1972, the first year of the period when shark attacks have been seen consistently year after year. In the fall data there is a direct relationship between the number of shark attacks and the number of seals ($r = 0.895$; $P < 0.01$). The ratio of attacks to the number of seals, except during spring and the 1979 seal breeding season, has remained at about 0.01-0.02.

Shark attacks during the elephant seal breeding season (winter) have been observed less often than during the fall but they may be increasing during that period, too, if the 1977-79 seasons are any indication. Interestingly, attacks were first seen during winter in the year when the elephant seal population surpassed 120 animals (1978), the same population level that occurred in conjunction with the first fall sighting of elephant seal/shark interactions (1972). This further indicates a density-dependent relationship between shark predation and elephant seal populations.

Acknowledgments

The Farallon Island field station of the Point Reyes Bird Observatory was supported financially by members and donors and by contracts from various agencies. In addition to our members, we wish especially to thank the Lucius M. Beebe Foundation, Charles E. Merrill Trust, McNaughton Foundation, Dean Witter Foundation, San Francisco Foundation, Packard Foundation, Standard Oil of California, and the U.S. Fish and Wildlife Service. Marine mammal observations from 1975 to 1979 were under contract from the Marine Mammal Commission. We also wish to thank the U.S. Coast Guard and particularly the Oceanic Society for logistic support. William I.

Follett kindly reviewed some photographs that we took of sharks, thus confirming our identifications, and checked an earlier version of this paper.

Literature Cited

AINLEY, D. G., AND T. J. LEWIS.
1974. The history of Farallon Island marine bird populations, 1854-1972. Condor 76:432-446.

BASS, A. J.
1978. Problems in studies of sharks in the southwest Indian Ocean. *In* E. S. Hodgson and R. F. Mathewson (editors), Sensory biology of sharks, skates, and rays, p. 545-549. Off. Nav. Res., Arlington.

BOLIN, R. L., AND D. P. ABBOTT.
1963. Studies on the marine climate and phytoplankton of the central coastal area of California, 1954-1960. Calif. Coop. Oceanic Fish. Invest. Rep. 9:23-45.

LE BOEUF, B. J., D. G. AINLEY, AND T. J. LEWIS.
1974. Elephant seals on the Farallones: population structure of an incipient breeding colony. J. Mammal. 55: 370-385.

O'GOWER, A. K., AND A. R. NASH.
1978. Dispersion of the Port Jackson shark in Australian waters. *In* E. S. Hodgson and R. F. Mathewson (editors), Sensory biology of sharks, skates, and rays, p. 529-544. Off. Nav. Res., Arlington.

PIEROTTI, R. J., D. G. AINLEY, T. J. LEWIS, AND M. C. COULTER.
1977. Birth of a California sea lion on southeast Farallon Island. Calif. Fish Game 63:64-66.

DAVID G. AINLEY
CRAIG S. STRONG
HARRIET R. HUBER
T. JAMES LEWIS
STEPHEN H. MORRELL

Point Reyes Bird Observatory
Stinson Beach, CA 94970

IN SITU OBSERVATIONS ON REPRODUCTIVE BEHAVIOR OF THE LONG-FINNED SQUID, *LOLIGO PEALEI*

There are several published accounts of reproductive behavior, including copulation and egg laying, of the long-finned squid, *Loligo pealei* Lesueur, in the laboratory (Drew 1911; Arnold 1962); but with the exception of Stevenson's (1934) field observations of *L. pealei*'s behavior around an egg mass, no in situ observations of egg-laying behavior have been documented for this species. Field and laboratory observations of reproductive behavior have been made for the California market squid, *L. opalescens* (McGowan 1954; Fields 1965; Hobson 1965; Hurley 1977), the tropical arrow squid, *L. plei* (Waller and Wicklund 1968), *L. bleekeri* (Hamabe and Shimizu 1957), *L. vulgaris* (Tardent 1962), the broad squid, *Sepioteuthis bilineata* (Larcombe and Russell 1971, and *S. sepioidea* (Arnold 1965). However, each species' in situ egg-laying behavior differed from the behavior we observed in *L. pealei*.

Observations

Each summer *L. pealei* and its egg masses are common in shallow coves along the coast of Rhode Island, such as our study site at Fort Wetherill on Conanicut Island in Narragansett Bay. Scuba divers, including ourselves, have observed squid to be numerous in these areas, particularly at night when they occur singly or in small, loosely formed schools.

On 16 June 1979, at 1230 h on an incoming tide (temperature 14.5°-15.0° C, depth 6 m) using scuba we observed a large squid egg mass (50-60 cm across) attached to one side of a small boulder. The surrounding area was a sandy/mud bottom with unattached fragments of the seaweeds *Ulva lactuca*, *Laminaria* sp., and *Porphyra* sp. Because the egg mass was larger than the 12-15 cm masses we regularly see in this area while diving, we spent some time observing it. Squid began to appear at the limit of the water visibility (about 4.0 m) and moved toward the egg mass in a semicircle. They stopped about 2.5-3.0 m from the mass and remained stationary approximately 1-m off the bottom. The squid were in well-defined pairs with the smaller females (mantle length 16-18 cm) parallel to and on the left of each male (20-22 cm) as we faced them (Figure 1). Eight pairs were visible at that time. The animals had moderate pigmentation over the mantles, but we did not observe the distinctive spots of color at the base of the arms as were reported by Arnold (1962), nor did we observe color changes during the observation period. Contrary to McGowan's (1954) observations on *L. opalescens*, all of the animals appeared to be in good condition; no torn epithelium was obvious and no dead or dying individuals had been seen in the area of the egg mass or anywhere else in the cove during the hour-long dive.

One pair of squid at a time approached the egg mass with their arms held forward and tentacles extended. Because of our position directly facing the squid, it was impossible to observe the beginnings of an egg finger protruding from the funnel as Drew (1911) and Tardent (1962) had observed in

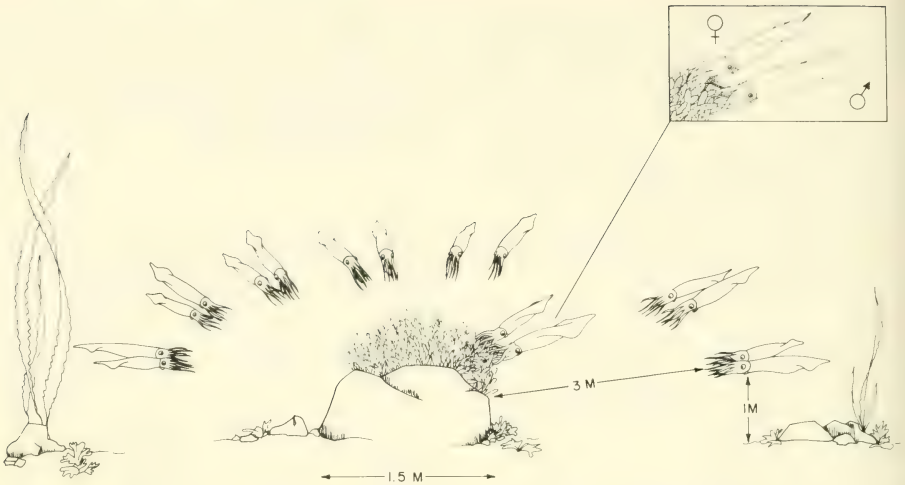


FIGURE 1.— Pairs of squid formed a semicircle and one pair at a time approached the egg mass. The female and male intertwined arms as they extended them into the egg mass. We surmise that the female was depositing an egg capsule and that the male was exhibiting parental care or "grooming" behavior. Water depth was 6 m.

L. pealei and *L. vulgaris* held in aquaria. However, comparing the behavior of the animals with that described in literature on squids' reproductive behavior, we concluded that the females were depositing egg capsules. They intertwined arms as they extended them into the egg mass. The arms of the male appeared to move delicately over and among the existing fingers of eggs (Figure 1). Each pair that approached the egg mass stayed 2-4 s then moved backward into the same position it had previously occupied in the semicircle. At that time another pair moved forward. There did not appear to be any order in which pairs approached the egg mass; however, no more than one pair approached at any given time. The same pair approached more than once.

Although most accounts indicate that copulation occurs just before egg deposition, our observations cannot substantiate this because egg laying had already commenced. No agonistic behavior which is often associated with reproduction was evident during the 10-min observation period.

Discussion

The social hierarchy involving egg deposition differs from species to species. Observations of *L. opalescens* and *L. plei* in the field indicate that once copulation occurs, individual pairs break apart and the female approaches the egg mass and deposits a capsule alone, although Hurley (1977) did observe an *L. opalescens* male pushing a female toward an egg mass. *Sepioteuthis sepioidea* remains paired after copulation, but only the female approaches the egg mass during egg laying (Arnold 1965). Larcombe and Russell (1971) reported that *S. bilineata* also remains paired, but the male escorts the female to the egg mass. However, the male assumes a protective role and follows about 0.5 m behind and above the female so he is between her and the other squid during the 2 s period in which she deposits a capsule. In contrast, *L. pealei* pairs formed and maintained a semicircle throughout egg laying (Figure 1). One pair at a time approached the egg mass; the male did not appear to assume a protective role, but might have been involved in "grooming" such as Tardent (1962) described for *L. vulgaris* held in an aquarium. Parental care or guarding egg masses has been documented for *L. pealei* by Stevenson (1934), who noted that both solitary males and pairs patrolled and guarded an egg mass. Similar guarding behavior has also been reported for *L. opalescens* (Hurley 1977).

Although there are similarities in reproductive behavior among several squid species, our observations of *L. pealei* indicate a social structure which is well defined and different from that described for other species with the possible exception of *S. bilineata* and *S. sepioidea*. Since there are relatively few published accounts of in situ copulation and egg-laying activities, it is difficult to know what is normal and what might be altered behavior patterns due to the presence of human observers, submersibles, lights, etc. However, our observations and those of other divers, including two in the same area a week earlier who reported 12-15 pairs of squids in a semicircle (Turco[1]), indicate that the social structure associated with egg-laying behavior is not an isolated phenomenon, but a pattern which is recurrent in populations of *L. pealei* which frequent New England coastal waters in the summer.

Acknowledgments

The authors extend their gratitude to Roger Hanlon for his review of the manuscript. We also thank William K. Macy III for his help during the development of the manuscript. We are grateful to Lianne Armstrong, who prepared the illustration, and to Jennie Dunnington for typing the manuscript.

Literature Cited

ARNOLD, J. M.
1962. Mating behavior and social structure in *Loligo pealii*. Biol. Bull. (Woods Hole) 123:53-57.
1965. Observations on the mating behavior of the squid *Sepioteuthis sepioidea*. Bull. Mar. Sci. 15:216-222.

DREW, G. A.
1911. Sexual activities of the squid *Loligo pealii* (Les.). I. Copulation, egg-laying and fertilization. J. Morphol. 22:327-359.

FIELDS, W. G.
1965. The structure, development, food relations, reproduction, and life history of the squid *Loligo opalescens* Berry. Calif. Dep. Fish Game, Fish Bull. 131, 108 p.

HAMABE, M., AND T. SHIMIZU.
1957. The copulation behavior of Yariika, *Loligo bleekeri* K. Rep. Jpn. Sea Reg. Fish. Res. Lab. 3:131-136.

HOBSON, E. S.
1965. Spawning in the Pacific Coast squid, *Loligo opalescens*. Underwater Nat. 3(3):20-21.

HURLEY, A. C.
1977. Mating behavior of the squid *Loligo opalescens*. Mar. Behav. Physiol. 4:195-203.

LARCOMBE, M. R., AND B. C. RUSSELL.
1971. Egg laying behaviour of the broad squid, *Sepioteuthis bilineata*. N.Z. J. Mar. Freshwater Res. 5:3-11.

MCGOWAN, J. A.
1954. Observations on the sexual behavior and spawning of the squid, *Loligo opalescens*, at La Jolla, California. Calif. Fish Game 40:47-54.

STEVENSON, J. A.
1934. On the behaviour of the long-finned squid (*Loligo pealii* [Lesueur]). Can. Field-Nat. 48:4-7.

TARDENT, P.
1962. Keeping *Loligo vulgaris* L. in the Naples Aquarium. 1er Congrès International d'Aquariologie, Monaco—1960. Vol. A, p. 41-46.

WALLER, R. A., AND R. I. WICKLUND.
1968. Observations from a research submersible—mating and spawning of the squid, *Doryteuthis plei*. BioScience 18:110-111.

CAROLYN A. GRISWOLD
JEROME PREZIOSO

Northeast Fisheries Center Narragansett Laboratory
National Marine Fisheries Service, NOAA
R.R. 7A, South Ferry Road
Narragansett, RI 02882

[1]Anthony Turco, West Main St., North Kingstown, R.I., pers. commun. June 1979.

SPAWNING AND SEXUAL MATURITY OF GULF MENHADEN, *BREVOORTIA PATRONUS*[1]

Earlier studies of egg and larva collections (Turner 1969; Fore 1970; Christmas and Waller[2]) have shown that Gulf menhaden, *Brevoortia patronus*, which range throughout the northern Gulf of Mexico from Cape Sable, Fla., to Veracruz, Mexico, spawn from about October to March from near shore to about 97 km offshore at depths of from 2 to 111 m. There have been two previous studies to determine the age of spawning, the number of ova produced, and the peak time of ovary maturation (Suttkus and Sundararaj 1961; Combs 1969). Our objectives in the present study were to: 1) estimate the minimum number of maturing ova for specific age-groups and size groups, 2) estimate the percentage of fish that spawn at each age, 3) determine the time of spawning, and 4) determine the frequency of spawning.

Gulf menhaden make annual inshore-offshore movements. The larvae spend 3-5 wk in offshore waters before moving into estuaries where they

[1]Southeast Fisheries Center Contribution No. 81-12B.

[2]Christmas, J. Y., and R. S. Waller. 1975. Location and time of menhaden spawning in the Gulf of Mexico. Unpubl. manuscr., 20 p. Gulf Coast Res. Lab., Ocean Springs, Miss. (NMFS contract no. 03-4-042-24).

transform into the adult form (Reintjes 1970). The following autumn the juveniles, ranging in fork length from about 55 to 130 mm FL, migrate from the estuaries to offshore waters (Tagatz and Wilkens 1973), along with all other age-groups that are moving from inshore waters of the gulf at this time. Fish of all age-groups migrate to inshore waters again the following spring.

While in inshore waters, age 1 and older Gulf menhaden are subject to an intensive purse seine fishery that extends from Florida to eastern Texas from about mid-April to early October. The fish are processed into meal, oil, and solubles at plants in Mississippi and Louisiana.

During the purse seine season Gulf menhaden are sexually inactive. Therefore, gonads collected at that time are of no use for fecundity studies. The only source of Gulf menhaden during the spawning season is the offshore groundfish trawl fishery, which takes Gulf menhaden incidentally along with the primary species. Catches are landed at plants in Mississippi and Louisiana and processed as canned pet food (Roithmayr 1965). The number of Gulf menhaden taken varies, but is never large. From October 1976 to February 1977, 241 females (124-257 mm FL) and 516 males (113-240 mm FL) were collected from the groundfish landings. After January, we were able to collect only 4 maturing females in February and none in March or April.

To assure that Atlantic menhaden, *B. tyrannus*, were assigned to the correct year class, June and Reintjes (1959) developed specific criteria for assigning fish to year classes on the basis of annulus formation. These criteria also were adopted when the investigation of Gulf menhaden was begun in 1964. March 1 was designated as an arbitrary date on which all fish of a given year class were advanced 1 yr in age, regardless of whether or not a new annulus had formed. Since all fish used in this study were collected from October to February, an age-1 fish is one that has one annulus, but has completed two growing seasons; an age-2 fish has two annuli but has completed three growing seasons.

All fish were caught in the northern Gulf of Mexico from lat. 28°35′ to 30°15′ N and from long. 87°45′ to 91°28′ W. Fork lengths were measured to the nearest millimeter and wet weights to the nearest 0.1 g. Scale samples for aging were taken from the left side of the body along the midline and below the origin of the dorsal fin. Paired gonads were preserved in a 10% buffered Formalin[3] solution.

Stages of Sexual Maturity

Preserved gonads were blotted to remove excess moisture and weighed to the nearest 0.01 g. A sample of 0.1 g or less was cut from the central portion of an ovary and examined microscopically to describe morphology of developing ova and to determine the mean diameter of the largest ova present.

Four groups of ova were found in the most advanced ovaries, while only one to three groups were found in less developed ovaries. Immature ova were under 0.20 mm in diameter, translucent, and contained an irregular spherical nucleus. Intermediate ova ranged from 0.20 to 0.35 mm and had a dark or opaque center surrounded by a wide sphere of dull yellowish to brownish speckling. Maturing ova were 0.36 to 0.72 mm, opaque, and had an outer translucent covering or tissue. Ripe ova were similar to maturing ova except they were >0.72 mm.

Three stages of sexual maturity were recognized on the basis of the most advanced group of ova present: immature, intermediate, and maturing. Fish classified as maturing contained either maturing or both maturing and ripe ova. All maturing or ripe ova in a sample were counted and about 100 were selected randomly and measured for diameter.

Age and Size of First Spawning

Gulf menhaden <135 mm can be considered as age-0 fish (Nicholson and Schaaf 1978). All fish <100 mm FL that we examined showed no evidence of maturing ova. Through December, 63% of age-1 fish and 71% of all fish age 2 or older in our samples contained maturing ova. By January all fish age 1 or older contained maturing ova (Table

[3]Reference to trade name does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Number of female Gulf menhaden sampled from October 1976 to February 1977 by age, month, and stage of sexual maturity (immature or mature).

Month	Age 1		Age 2		Age 3		Age 4
	Immature[1]	Mature	Immature	Mature	Immature	Mature	Mature
Oct.	5	6	3	10			
Nov.	4	15		3			
Dec.	4	1	4	3	1	3	1
Jan.		19		3		2	
Feb.		3		1			

[1]Fish with intermediate ova (as the largest ova present) were included in this category.

TABLE 2.—Number of female Gulf menhaden sampled from October 1976 to February 1977 by fork length, month, and stage of sexual maturity (immature or mature).

Fork length (mm)	Oct.		Nov		Dec.		Jan.	Feb.
	Immature[1]	Mature	Immature	Mature	Immature	Mature	Mature	Mature
120-129	2							
130-139	1							
140-149			1	1				
150-159			2	3	1		1	
160-169	5	1	2	8	1		6	1
170-179	7	15	2	15	1	2	10	2
180-189	6	17		15			2	
190-199	5	20		12	2		2	
200-209	3	14		11	3	1	3	1
210-219	1	3		1		4	1	
220-229		3		1	1	2	2	
230-239		1		4		1	5	
240-249				1		1	1	
250-259							1	

[1]Fish with intermediate ova (as the largest ova present) were included in this category.

1). For both aged and unaged fish >140 mm that we examined, 73% contained maturing ova in October, 91% in November, 55% in December, and 100% in January and February (Table 2). From this information we concluded that Gulf menhaden spawn for the first time at age 1, after they have completed two seasons of growth, and then continue to spawn each year thereafter.

Time and Frequency of Spawning

Previous studies of egg and larva collections (Turner 1969; Fore 1970; Christmas and Waller footnote 2) and of increases in gonad weights (Suttkus and Sundararaj 1961; Combs 1969) have indicated that spawning begins in October and ends about March. Our data also show that spawning occurs within this time period. For each month we plotted the mean gonad weight as a percentage of body weight for those fish we were able to age (Figure 1). For females the means, which were already high in October, indicating that gonadal development had begun, increased in November and December and then decreased in January and February. Generally, males followed the same pattern as females when both aged and unaged were combined (Figure 2). We can not explain why the relative gonad weights of age-1 females were higher than those of older fish, unless some of the older fish had partially spawned by the time they were collected, thereby decreasing their gonad weight.

The number of times an individual fish will spawn during a season may be inferred from the difference in size between groups of ova. If there is

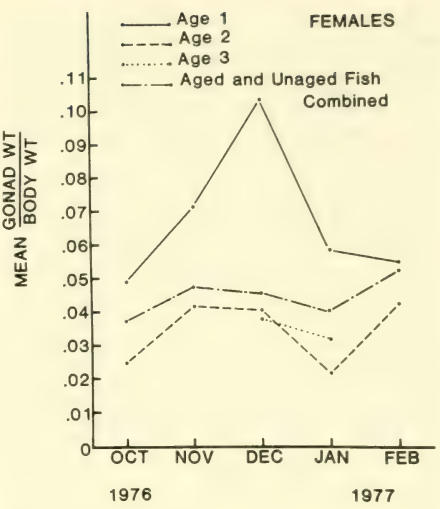


FIGURE 1.—Relation between mean of gonad weight/body weight and month for unaged and different age-groups of female Gulf menhaden.

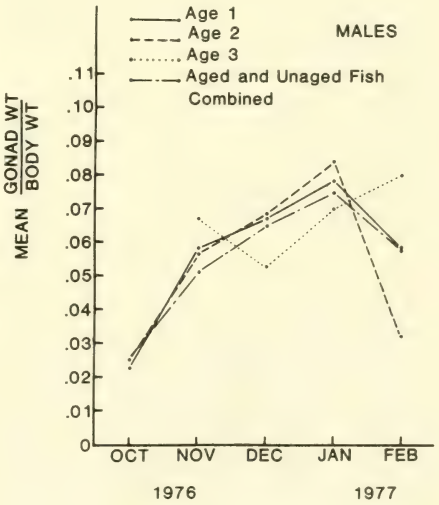


FIGURE 2.—Relation between mean of gonad weight/body weight and month for unaged and different age-groups of male Gulf menhaden.

a large difference in size between immature ova, developing intermediate ova, and maturing ova, the spawning period will be short and definite. If there is only a gradual change in size between these groups of ova, individual fish may spawn several times over an extended period (Hickling and Rutenberg 1936; de Vlaming 1974).

Since there was a gradual change in size between groups of ova, and since the number and diameter of maturing or ripe ova for fish of the same length varied considerably, we inferred that Gulf menhaden were intermittent, or fractional spawners. The number of maturing ova did not change markedly from month to month, or even within the same month. The ripe ova, after being spawned, probably are replaced by a group of the largest maturing ova which in turn are replaced by a group of intermediate ova. Perhaps four or five different groups of ova ripen and are spawned during a single spawning season, although the exact number cannot be estimated.

Higham and Nicholson (1964) stated that, from available evidence, it is impossible to decide conclusively the frequency of spawning of individual Atlantic menhaden but they favored the hypothesis of maturation and fractional spawning of more than one group of ova during the season.

Combs (1969) concluded that *B. patronus* spawns several times from October to February. He found that over a period of months spawnable oocytes occurred together with advanced stages of ova that were potentially spawnable. He described the histological events in the development of Gulf menhaden ova from formation to maturity and found that once the provisional yolk had formed, ova lost all potential to remain in the ovary and had to complete their development prior to spawning or be aborted.

Number of Ova Spawned

Since analysis of variance tests showed no significant difference in the size or number of maturing ova in gram samples from the left and right ovaries, we used either ovary for measurements and counts. (Counts were made of the number of maturing ova in a sample of 0.1 g or less from an ovary.) The number of maturing or ripe ova in each female was estimated by dividing the combined weight of the left and right ovaries by the sample weight and multiplying this number by the number of maturing or ripe ova in the sample.

If fractional spawning occurs, the number of ova estimated to have been spawned by fish of any given age or size would necessarily be minimal, since some ova probably would have been spawned by the time some ovaries were collected. Fractional spawning also would increase the variability in the number of ova estimated for fish of the same age or size (Bagenal and Braum 1971). Of the 70 maturing females that we could age, 44 were age 1, 20 were age 2, 5 were age 3, and 1 was age 4. The mean number of ova and its standard error for each age-group respectively were 37,100±3,467; 47,900±5,038; 61,800±9,486, and 151,000.

Three relationships that are most useful in explaining and understanding population dynamics of a species are those of fecundity with age, length, and weight. To determine what mathematical models would be most appropriate in describing these relations, we used Statistical Analysis System[4] to test various statistical regression models. We chose those which had the greater r^2 values and the minimum deviations from the regression line. In the following models F = fecundity, A = age, L = fork length, and W = body weight. For fecundity on age (Figure 3):

[4]Statistical Analysis System; Barr, Goodnight, Sall and Helwig, SAS Institute Inc., P.O. Box 10066, Raleigh, NC 27506.

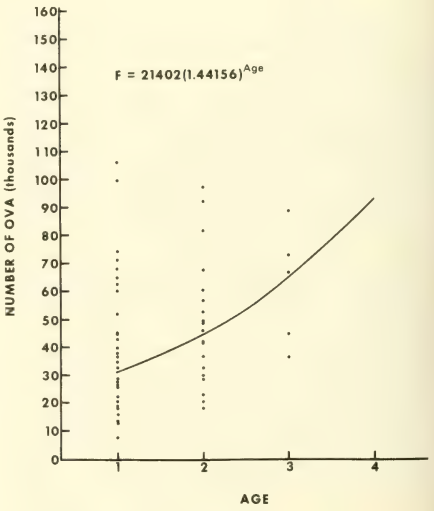


FIGURE 3.—Relation between number of maturing ova and age for Gulf menhaden.

$$\log_e F = 9.9713 + 0.3657(A)$$
$$(r^2 = 0.1804,\ s_{y \cdot x} = 0.5466).$$

For fecundity on fork length (Figure 4):

$$\log_e F = -9.8719 + 3.8775(\log_e L)$$
$$(r^2 = 0.6490,\ s_{y \cdot x} = 0.3751).$$

For fecundity on weight:

$$F = 12{,}064.2908 + 374.8848(W)$$
$$(r^2 = 0.4445,\ s_{y \cdot x} = 20{,}427.0752).$$

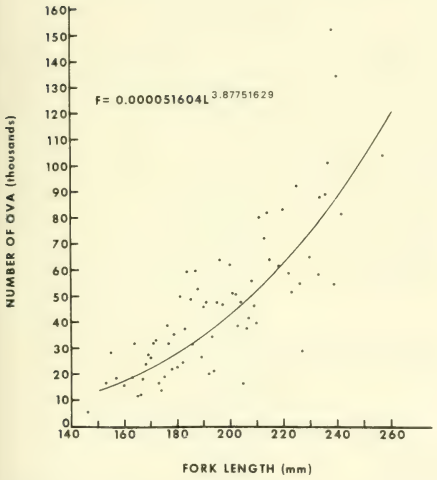


FIGURE 4.—Relation between mean number of maturing ova and fork length for Gulf menhaden.

Literature Cited

BAGENAL, T. B., AND E. BRAUM.
1971. Eggs and early life history. *In* W. E. Ricker (editor), Methods for assessment of fish production in fresh waters, 2d ed., p. 166-198. IBP (Int. Biol. Programme) Handb. 3.

COMBS, R. M.
1969. Embryogenesis, histology and organology of the ovary of *Brevoortia patronus*. Gulf. Res. Rep. 2:333-434.

DE VLAMING, V. L.
1974. Environmental and endocrine control of teleost reproduction. *In* C. B. Schreck (editor), Control of sex in fishes, p. 13-83. Va. Polytech. Inst. State Univ., VPI-SG-74-01.

FORE, P. L.
1970. Oceanic distribution of eggs and larvae of the Gulf menhaden. *In* Report of the Bureau of Commercial Fisheries Biological Laboratory, Beaufort, N.C., for the fiscal year ending June 30, 1968, p. 11-13. U.S. Fish Wildl. Serv. Circ. 341.

HICKLING, C. F., AND E. RUTENBERG.
1936. The ovary as an indicator of the spawning period in fishes. J. Mar. Biol. Assoc. U.K. 21:311-317.

HIGHAM, J. R., AND W. R. NICHOLSON.
1964. Sexual maturation and spawning of Atlantic menhaden. U.S. Fish Wildl. Serv., Fish. Bull. 63:255-271.

JUNE, F. C., AND J. W. REINTJES.
1959. Age and size composition of the menhaden catch along the Atlantic coast of the United States, 1952-1955; with a brief review of the commercial fishery. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 317, 65 p.

NICHOLSON, W. R., AND W. E. SCHAAF.
1978. Aging of Gulf menhaden *Brevoortia patronus*. Fish. Bull., U.S. 76:315-322.

REINTJES, J. W.
1970. The Gulf menhaden and our changing estuaries. Proc. Gulf Caribb. Fish. Inst. 22:87-90.

ROITHMAYR, C. M.
1965. Industrial bottomfish fishery of the northern Gulf of Mexico, 1959-63. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 518, 23 p.

SUTTKUS, R. D., AND B. I. SUNDARARAJ.
1961. Fecundity and reproduction in the largescale menhaden, *Brevoortia patronus* Goode. Tulane Stud. Zool. 8:177-182.

TAGATZ, M. E., AND E. P. H. WILKENS.
1973. Seasonal occurrence of young Gulf menhaden and other fishes in a northwestern Florida estuary. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-672, 14 p.

TURNER, W. R.
1969. Life history of menhadens in the eastern Gulf of Mexico. Trans. Am. Fish. Soc. 98:216-224.

ROBERT M. LEWIS

Southeast Fisheries Center Beaufort Labortory
National Marine Fisheries Serivce, NOAA
P.O. Box 570
Beaufort, NC 28516

CHARLES M. ROITHMAYR

Southeast Fisheries Center Pascagoula Laboratory
National Marine Fisheries Service, NOAA
P.O. Drawer 1207
Pascagoula, MS 39567

FOOD OF THE PACIFIC WHITE-SIDED DOLPHIN, *LAGENORHYNCHUS OBLIQUIDENS*, DALL'S PORPOISE, *PHOCOENOIDES DALLI*, AND NORTHERN FUR SEAL, *CALLORHINUS URSINUS*, OFF CALIFORNIA AND WASHINGTON

Our knowledge of the feeding habits of the Pacific white-sided dolphin, *Lagenorhynchus obliquidens*, and the Dall's porpoise, *Phocoenoides*

dalli, is based on examination of the stomach contents of stranded animals, animals accidentally taken in commercial fishing gear, those taken in the western Pacific commercial fishery, and animals that died during capture attempts. Of these only a few were normally feeding animals taken at sea, whose stomach contents were thoroughly examined. Fishes and squids previously identified from stomachs of dolphins and porpoises by various investigators are listed in Table 1.

This paper documents the stomach contents of 44 Pacific white-sided dolphin and 9 Dall's porpoise collected at sea off California and Washington. All animals were collected by the authors during pelagic fur seal studies with the exception of three dolphins which were collected by a staff biologist during whale research voyages off California. Comparisons of stomach contents are made between the Pacific white-sided dolphin, Dall's porpoise, and northern fur seal, *Callorhinus ursinus*, collected near the same locations and usually on the same day. Mention of the dolphin, porpoise, and seal in this paper refers to the above-named species only unless noted otherwise.

The Pacific white-sided dolphin ranges the eastern North Pacific Ocean, from Baja California

TABLE 1.—List of fishes and squids previously identified in stomachs of Pacific white-sided dolphin and Dall's porpoise from the North Pacific Ocean by localities.

Locality and species	Reference source	
	Pacific white-sided dolphin	Dall's porpoise
California:		
Pacific herring, *Clupea harengus pallasi*		Loeb 1972
Pacific sardine, *Sardinops sagax*	Higgins 1919	
Northern anchovy, *Engraulis mordax*	Brown and Norris 1956; Norris and Prescott 1961; Fiscus and Niggol 1965; Fitch and Brownell 1968	Loeb 1972
Night smelt, *Spirinchus starksi*		Loeb 1972
California smoothtongue, *Bathylagus stilbius*		Loeb 1972
Pinpoint lampfish, *Lampanyctus regalis*		Loeb 1972
Blue lanternfish, *Tarletonbeania crenularis*		Loeb 1972
Pacific whiting, *Merluccius productus*	Best 1963; Fiscus and Niggol 1965; Fitch and Brownell 1968	Norris and Prescott 1961; Best 1963; Loeb 1972
Cusk-eel, *Otophidium taylori*		Loeb 1972
Eelpouts, Zoarcidae		Loeb 1972
Grenadier, Macrouridae		Loeb 1972
Pacific saury, *Cololabis saira*	Houck 1961	
Jack mackerel, *Trachurus symmetricus*	Scheffer 1953; Norris and Prescott 1961; Houck 1961	Norris and Prescott 1961
Pacific pompano, *Peprilus simillimus*		Loeb 1972
Rockfish, *Sebastes* spp., juvenile		Loeb 1972
Sablefish, *Anoplopoma fimbria*, juvenile		Loeb 1972
Snailfish, *Liparis* sp.		Loeb 1972
Pacific sanddab, *Citharichthys sordidus*		Loeb 1972
Eels, Anguilliformes		Loeb 1972
Squid, *Loligo opalescens*	Brown and Norris 1956; Ridgway 1966	Norris and Prescott 1961; Loeb 1972
Squid, *Abraliopsis* sp.		Loeb 1972
Squid, *Gonatus* sp.	Fiscus and Niggol 1965	Loeb 1972
Squid, *Onychoteuthis borealijaponicus*		Loeb 1972
Octopus, *Octopus bimaculatus*		Loeb 1972
British Columbia:		
Pacific herring, *Clupea harengus pallasi*		Cowan 1944
Gulf of Alaska:		
Capelin, *Mallotus villosus*		Scheffer 1953
Japan:		
Anchovy, *Engraulis japonica*	Hotta et al. 1969	
Sudidae, *Paralepis* sp.		Wilke and Nicholson 1958
Lanternfish, Myctophidae—Scopelidae	Wilke et al. 1953	Wilke et al. 1953
Lanternfish, *Notoscopelus* sp.		Wilke and Nicholson 1958
Lanternfish, *Diaphus* sp.		Wilke and Nicholson 1958
Lanternfish, *Tarletonbeania taylori*		Wilke and Nicholson 1958
Lanternfish, *Lampanyctus* sp.		Wilke and Nicholson 1958
Lanternfish, *Myctophum* sp.		Wilke and Nicholson 1958
Cod, *Laemonema longipes*		Wilke and Nicholson 1958
Hake, *Laemonema morsum*		Wilke et al. 1953
Mackerel, *Scomber japonicus*	Wilke et al. 1953	
Squid, *Watasenia scintillans*	Wilke et al. 1953	
Squid, *Omnastrephes sloani pacificus*	Hotta et al. 1969	Wilke and Nicholson 1958
Northwestern Pacific and western Bering Sea:		
Sockeye salmon, *Oncorhynchus nerka*		Mizue et al. 1966
Unidentified small fish		Koga 1969
Unidentified fish		Mizue and Yoshida 1965; Mizue et al. 1966
Squids		Mizue and Yoshida 1965; Mizue et al. 1966; Koga 1969
Shrimp		Mizue and Yoshida 1965; Mizue et al. 1966; Koga 1969

northward in the summer to the Gulf of Alaska; it ranges the western North Pacific Ocean, from Japan northward to the Kurile Islands (National Marine Fisheries Service 1978). During pelagic fur seal research voyages off California (1958-66) and Washington (1958-72), 767 pods of dolphin totalling 8,803 animals were sighted[1] (297 pods, 5,555 dolphin, and 490 pods, 3,248 dolphin, respectively). Dolphin pod size ranged from 1 to 1,000+ animals. The dolphin reported here were collected from pods ranging from 4 to 300 animals.

The Dall's porpoise ranges the North Pacific Ocean from northern Baja California and Japan in the south to the Bering and Okhotsk Seas, moving into the southern portion of its range during winter. The porpoise usually occur in smaller groups than do the dolphin. During pelagic fur seal research cruises off California and Washington, 868 pods totalling 3,575 porpoise were sighted (657 pods, 2,845 porpoise, and 211 pods, 730 porpoises, respectively). Porpoise pods generally contained fewer than 20 animals. The porpoise reported here came from pods of three to five animals. Sightings and collections of dolphin and porpoise were obtained during 388 d at sea off California in 1958-66 and 368 d at sea off Washington in 1958-72.

The northern fur seal ranges across the subarctic waters of the North Pacific Ocean and numbers about 1.8 million animals (Lander and Kajimura 1976). Most seal are found near their breeding islands in the Bering and Okhotsk Seas from July into early November except for the very small San Miguel Island, Calif., population that numbers about 2,000 animals. In the eastern North Pacific Ocean few adult males are found south of the Gulf of Alaska. Mature females and immature males and females begin to appear in coastal waters between British Columbia and central California in late November and early December, the pups slightly later in January or February. The movement is generally southward along the continental shelf and slope in January into March with some animals ranging south to about lat. 32° N; however, most of the wintering population can be found between about lat. 35° and 49° N. Some northward migration out of this region may begin as early as March. Most wintering seal are found from over the continental shelf seaward as much as several hundred miles (Fiscus 1978).

Northern fur seal are most frequently observed alone rather than in company with other seal of their species; however, concentrations do occur in areas of abundant food supply. In 1966 (January-March) off California when most of the dolphin and porpoise were collected, 1,441 groups of seal were observed, of which 31% were single animals; 22% were in groups of 2; 16.9% in groups of 3; 10.5% in groups of 4; and 10.2% in groups of 5-20 (Marine Mammal Biological Laboratory 1969).

In 1967-68 (November-February) off Washington, when most of the dolphin and porpoise were collected, 669 groups of seal contained 40.8% single animals; 24.9%, groups of 2; 13.6%, groups of 3; 9.3%, groups of 4; and 14%, groups of 5-9 (Marine Mammal Biological Laboratory 1970).

There are no reliable estimates of the numbers of Pacific white-sided dolphin and Dall's porpoise that inhabit the eastern Pacific offshore waters from California to Washington; however, these two species are the most frequently sighted cetaceans in these waters.The northern fur seal is the only pinniped regularly inhabiting this region. It is a seasonal visitor, from December through May; as many as 500,000 may be here during the peak of the wintering period (Fiscus 1979).

Methods

Hand harpoons or shotguns were used to collect the Pacific white-sided dolphin and Dall's porpoise as they rode the bow wave of the research vessel or dory. Northern fur seal were collected from the vessel or dory with shotguns. The dolphin and porpoise were taken off California, 1-130 km seaward of the continental shelf; those from Washington waters were taken near or over the continental shelf.

Standard measurements and weights of each cetacean and seal were recorded (American Society of Mammalogists, Committee on Marine Mammals 1961, 1967). Reproductive tracts, skulls, stomachs, and tissue samples were collected. Stomachs were tied with string at the esophagus and pyloris and then injected with and preserved in 10% Formalin[2] for laboratory examination. The contents of each stomach were gently washed and drained in a small mesh sieve. The stomach rugae

[1]NMFS, Natl. Mar. Mammal Lab. 1958-74. Birds and mammals observed at sea. Unpubl. data listing, various pagination. Natl. Mar. Mammal Lab., Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE., Seattle, WA 98115.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

were carefully checked for squid beaks, fish otoliths, and other small remains of food items. After excess fluid was drained off, the total weight of stomach contents was recorded and a total volume determined by water displacement. Individual food items were identified, counted, and the percentage of the total volume represented by each type of food item estimated. Fragments of prey species may remain in the stomachs of these animals from 12 to 24 h after feeding; hence hard parts of prey species consumed over the shelf, such as chitinous beaks of squids, fish otoliths, and particularly dense fish bones, may still persist in the stomachs of animals taken well offshore of the shelf. Identification was made by comparison with reference specimens and to descriptions in taxonomic keys or other references.

Of the 33 dolphin taken off California, 25 were females (9 adult, 15 subadult, 1 probably adult) and 8 were males (3 adult, 5 subadult). Of 11 dolphin taken off Washington, 8 were females (2 adult, 6 subadult) and 3 were males (1 adult, 2 subadult). All nine of the Dall's porpoise were adults.

Scientific names of marine mammals follows Marine Mammal Commission[3]; of fish, Bailey et al. (1970) and Fitch and Lavenberg (1971); of cephalopods, Young (1972).

Results

Pacific White-Sided Dolphin and Northern Fur Seal

Northern anchovy, *Engraulis mordax*, was the most frequently occurring fish in the stomachs of white-sided dolphin and northern fur seal taken in all collection months and across the latitudinal range of the collections off California. Most dolphin were taken off central California between Pt. Conception and Pt. Reyes in the following numbers by month: 1 in January, 11 in February, 18 in March, 2 in June, and 1 in December. Seal used in comparisons were taken in the same localities at the same times. Northern anchovy remains were identified from 58% (19 occurrences) of the dolphin stomachs and 32% (13 occurrences) of seal stomachs collected in the same localities.

Pacific whiting, *Merluccius productus*, was found in 33% (10 occurrences) of the dolphin stomachs and 34% (14 occurrences) of the seal stomachs. Pacific whiting was particularly important in the March 1966 collections at lat. 35° to 38° N (Morro Bay to San Francisco). Pacific saury, *Cololabis saira*, the third ranking fish, was found in 28% (9 occurrences) of the dolphin but in only 7% (3 occurrences) of the seal from the same area.

Squids of the family Gonatidae were the most frequently occurring cephalopods. Both *Loligo opalescens* (64% occurrence) and *Onychoteuthis borealijaponicus* (45% occurrence) were found in the dolphin stomachs in trace amounts only (beaks); however, both species are important seal prey. *Abraliopsis* sp. was identified only once in seal but found in 16 dolphin stomachs from seven collection locations off California. Stomachs of the nine dolphin collected 25 February 1966 off Pt. Reyes contained a greater variety of fishes and squids than those collected in other locations.

The food items consumed by 11 dolphin and 14 seal collected in the same locality off Washington show salmonids, *Oncorhynchus* spp., composed most of the stomach contents of 10 dolphin and 12 seal taken 25 and 26 February 1968 over the Astoria Canyon, approximately 37-44 km west of the Columbia River (8 occurrences in dolphin, 3 in seal). Flatfishes (Pleuronectidae) were present in one seal stomach. Squid beaks representing nine families, genera, or species of squids were identified from the stomachs of dolphin, but these taxa were of minimal importance in the stomachs of seal collected from the same area, occurring in only 4 of 12 stomachs. One dolphin, taken off the continental shelf, 25 April 1972, contained trace amounts of unidentified fishes and squids representing at least five genera. The stomachs of two seal collected in the same area the same day were empty.

Dall's Porpoise and Northern Fur Seal

The stomach contents of 9 Dall's porpoise and 17 northern fur seal taken from the same location off California and Washington from 1964 to 1968 were examined. One porpoise was taken in January off southern California and four were taken in February and one in April off central California. Three were taken off Washington, two in January (one taken in the entrance to the Strait of Juan de Fuca) and one in February. Off California, northern anchovy, Pacific whiting, Pacific saury, and squids, *L. opalescens* and *O. borealijaponicus*, formed major portions of the most recent feedings.

[3]Marine Mammal Commission. 1976. Marine mammal names. Unpubl. manuscr., 8 p. Marine Mammal Commission, 1625 Eye Street, NW., Wash., DC 20006.

Unidentified fishes and six species of squids were also found in trace amounts. The stomachs of three porpoise taken 56 km southwest of Pt. Reyes on 21 February 1966 contained no northern anchovy but did contain typical open ocean dwelling fishes and squids. Off Washington trace amounts of eulachon, *Thaleichthys pacificus*; rockfish, *Sebastes* spp.; sablefish, *Anoplopoma fimbria*; flatfish, Pleuronectidae; American shad, *Alosa sapidissima*; capelin, *Mallotus villosus*; and squids, *L. opalescens*, Gonatidae, *Gonatus* sp., and *O. borealijaponicus*, were found in stomachs of three porpoise.

Discussion

Distribution of Prey

Based on identified prey species, it appears that all three of the mammals feed in the epipelagic (0-200 m) and mesopelagic (200-1,000 m) zones of the ocean and that over the continental shelf, they may descend to the bottom (200 m or less) on occasion as demonstrated by the presence of demersal species in their stomachs. Many of the fishes and squids rise to or toward the surface at night, thereby becoming more readily available and perhaps ruling out the necessity for long, deep dives. Kooyman et al. (1976), reporting on fur seal diving behavior, indicated that dives between the surface and 20 m lasting <1 min may be for shallow feeding or travel and that dives between 20 and 140 m of 3.3-3.4 min duration may be hunting and feeding dives. They reported dives deeper than 140 m; the deepest reported dive lasted 5.4 min and reached 190 m. A study of blood oxygen levels of three genera of porpoise by Ridgway and Johnston (1966) reported that the Pacific white-sided dolphin cannot swim as fast and probably cannot dive as deep as the Dall's porpoise.

Prey Species

Off the California coast all three of the mammals feed primarily on small schooling fishes and cephalopods, including the northern anchovy, Pacific saury, and Pacific whiting. Other species of fish were probably taken as the opportunity arose. The primary fish species in dolphin collected off the Washington coast were salmonids (genus *Oncorhynchus*). Because the latter collection was made in a small area over a 3-d period, the taking of salmonids may have been opportunistic and short term rather than typical of more routine feeding. This sample is too small to conclude that a major predator-prey relationship exists between the Pacific white-sided dolphin and the salmonids.

Cephalopods are probably more important as prey species than indicated by the relative volume of stomach contents in the collection. Except for the chitinous beaks, cephalopods are probably more rapidly digested than fish. Marine mammals are more likely to feed on squids during the night because the vertical migration of many species brings them closer to the surface waters (Roper and Young 1975; Pearcy et al. 1977). Collection of dolphin during the day would give adequate time for digestion of fleshy parts, thus leaving the large numbers of indigestible chitinous beaks often found in stomachs.

The fishes and squids identified in the stomachs of the dolphin, porpoise, and seal taken during this study are presented in Table 2.

Stomach Capacity of Predators

The 44 Pacific white-sided dolphin were all adult or subadult animals, presumably with stomachs of maximum size. Eleven stomachs contained only trace amounts of food, and 33 contained food contents varying from 10 to 3,490 cm^3 (10-3,745 g).

The dolphin whose stomach contained the most food from California waters had eaten 68 anchovy (1,770 cm^3 or 1,895 g). Anchovy grow to 18-20 cm and may weight 57 g (Fitch and Lavenberg 1971).

Off Washington, the largest dolphin stomach examined contained the remains of nine salmon (including identifiable remains of four coho salmon and two pink salmon) which measured 26.0, 27.0, 31.0, 31.5, 31.5, 33.0, 33.0, 33.0, and 33.5 cm. The full stomach measured 40 cm long and 24 cm at the widest point (outside stomach dimensions), and the stomach contents represented 4.4% (3,490 cm^3 or 3,745 g) of the total body weight of the animal.

The largest stomach content from a Dall's porpoise off California contained 58 northern anchovy (1,000 cm^3 or 1,090 g). Off Washington, the largest stomach content contained fragments of five capelin, four eulachon, one flatfish (family Pleuronectidae), and trace amounts of squids (*Gonatus* sp. and Gonatidae) (130 cm^3 or 125 g). Five stomachs contained food volumes varying from 5 to 1,000 cm^3 (5-1,090 g) whereas four stomachs contained only trace amounts of food. Except for occasional

TABLE 2.—Size of fish and frequency of occurrence of fishes and cephalopods found in the stomachs of Pacific white-sided dolphin, Dall's porpoise, and northern fur seal[1] collected off California and Washington, 1964-72.

Taxon	Measurable length of fish in stomachs[2] (cm)	California			Washington		
		White-sided dolphin (33 coll.)	Dall's porpoise (6 coll.)	Northern fur seal ([3]41[4]10 coll.)	White-sided dolphin (11 coll.)	Dall's porpoise (13 coll.)	Northern fur seal ([3]14[2]7 coll.)
Fish:							
Pacific lamprey, *Entosphenus tridentatus*[5]	—	—	—	—	1	—	—
American shad, *Alosa sapidissima*	—	—	—	—	—	—	1
Pacific herring, *Clupea harengus pallasi*	28.5-31.3 (11)	—	—	—	—	—	—
Northern anchovy, *Engraulis mordax*	14.5-17.8 (19)	19	2	[3]13[4]5	—	—	—
Salmon, *Oncorhynchus* spp.[5]	—	—	—	—	8	—	2
Pink salmon, *O. gorbuscha*[5]	25.0-40.5 (3)	—	—	—	—	—	2
Chum salmon, *O. keta*[5]	—	—	—	—	1	—	1
Coho salmon, *O. kisutch*[5]	21.0-33.0 (5)	—	—	—	2	—	2
Chinook salmon, *O. tshawytscha*[5]	21.0-24.5 (2)	—	—	—	—	—	—
Capelin, *Mallotus villosus*	10.9-15.5 (26)	—	—	—	—	1	—
Eulachon, *Thaleichthys pacificus*[6]	15.3-20.5 (4)	—	—	—	—	1	1
California lanternfish, *Symbolophorus californiensis*[5]	—	1	—	—	—	—	—
Pacific saury, *Cololabis saira*[6]	—	9	1	3	—	—	—
Pacific whiting, *Merluccius productus*	—	10	2	[3]14[4]1	—	—	—
King-of-the-salmon, *Trachipterus altivelis*[5]	—	1	—	—	—	—	—
Jack mackerel, *Trachurus symmetricus*	—	1	—	—	—	—	—
Drum, *Sciaenidae*	—	—	—	1	—	—	—
Medusafish, *Icichthys lockingtoni*[5]	—	1	—	—	—	—	—
Rockfish, *Sebastes* spp.[5]	—	1	—	1	—	—	2
Sablefish, *Anoplopoma fimbria*	25.0 (1)	—	—	—	—	—	1
Pacific sanddab, *Citharichthys sordidus*[5]	—	1	—	—	—	—	—
Righteye flounder, Pleuronectidae[6]	—	—	—	—	—	1	1
Cephalopods:							
Squid, *Loligo opalescens*	—	21	1	[3]2[4]1	3	1	
Squid, *Abraliopsis* sp.[5]		16	3	1	11	—	—
Squid, *Octopoteuthis* sp.[5,6]		12	1	—	9	—	—
Squid, Gonatidae		14	2	[3]1[4]2	11	2	[3]1[4]2
Squid, *Gonatus* sp.		23	1	2	11	2	3
Squid, *Gonatopsis borealis*[5]		7	—	—	2	—	—
Squid, *Onychoteuthis borealijaponicus*[5]	—	15	2	4 1	11		1
Squid, *Chiroteuthis* sp.[5]		2	—	—	3	—	—
Squid, *Cranchiidae*[5]		3	1	—	3	—	—
Pelagic octopus, *Ocythoe tuberculata*[5]		2	—	—	—	—	—

[1]A complete list of prey species of the northern fur seal appears in North Pacific Fur Seal Commission Reports on Investigations, 1962, 1969, 1971, 1975.
[2]Length measurement of chinook salmon and sablefish is standard length, other measurements are total length. The numbers in parentheses indicate sample size.
[3]Northern fur seal in association with Pacific white-sided dolphin.
[4]Northern fur seal in association with Dall's porpoise.
[5]Identified for the first time as prey of the Pacific white-sided dolphin.
[6]Identified for the first time as prey of the Dall's porpoise

squid beaks, bone fragments, and otoliths, which were found in the fundic (or pyloric) stomach and the duodenal ampulla, all undigested or semidigested food items were found in the forestomach. Stomach volumes were highly variable depending on the time of day the animal was collected and the digestibility of the species of fish or squid ingested. Of 30 dolphin taken off California, those taken before 1000 h averaged more than twice the volume of food in their stomachs than those taken after 1000 h.

During the course of pelagic fur seal research, thousands of seal stomachs have been examined by the authors. The stomach containing the most food was from a 17-yr-old male collected in the eastern Bering Sea at 1330 h, 9 August 1968. The animal had consumed 13 walleye pollock, *Theragra chalcogramma*, and 4 squid, *Berryteuthis magister*. The contents weighed 9.8 kg (9,175 cm^3 volume representing 7.2% of body weight) with walleye pollock composing 80% (7,340 cm^3) of the total stomach volume. The stomach of an adult female fur seal contained food weighing 5.9 kg (5,565 cm^3 volume representing 13.1% of body weight). This 15-yr-old animal was collected at 0645 h on 19 April 1964 off California and had fed on 31 Pacific whiting.

The energy requirements of the northern fur seal are poorly known. Keyes (1968) reported that seal and other pinnipeds kept in captivity subsisted well on 6-12% of body weight daily, with vitamin supplements. Studies indicate possibly higher daily consumption rates among growing immature animals. Sergeant (1969) summarized the feeding rates per day of several captive cetaceans including two dolphin which consumed 7.9% of their body weight in herring and mackerel and a porpoise that consumed 11.3% of its body weight of mackerel. Ridgway (1972) reported food requirements in captive animals equalled 7-8% of body

weight/d for dolphin and 10-12% for porpoise. The species fed to these captive animals were not identified.

Size of Prey

Higgins (1919) mentioned a stomach containing six large Pacific sardine, *Sardinops sagax*, each about 30 cm long. Houck (1961) reported a dolphin with a stomach full of Pacific saury and with a 33 cm jack mackerel, *Trachurus symmetricus*, wedged in its throat. Unfortunately, no count of the Pacific saury was given. Fitch and Brownell (1968) reported that otoliths representing 29 Pacific whiting 40-50 cm long and 14 Pacific whiting about 20 cm long were recovered from a dolphin stomach. The sizes of fish in stomach contents were measured only from whole or nearly whole specimens or those with complete vertebral columns (Table 2). All salmon consumed by dolphin were generally immature, showing 0-age ocean growth, although a few showed 1, 2, and 3 ocean annuli.

Scheffer (1953) reported on stomach contents of two Dall's porpoise taken off Oregon, each of which contained four Pacific whiting about 45 cm long. These records represent the largest fish recovered from porpoise stomachs. Mizue et al. (1966) reported only one occurrence of sockeye salmon, *O. nerka*, from stomachs of 148 porpoise taken in conjunction with the high-seas salmon gill net fishery. No mention was made of the size of this fish, although they did state that adult salmon are probably not taken by animals of this species.

In our collections, there was no evidence of large fish being broken up prior to ingestion by either dolphin or porpoise. Captive bottlenose dolphin, *Tursiops truncatus*, have been observed to break up food species.[4] The teeth, jaw structure, and relative neck mobility of the white-sided dolphin are similar to those of the bottlenose dolphin and would allow such behavior in this species more so than in the Dall's porpoise. The maximum size of prey eaten is apparently limited by the predator's ability to capture and swallow whole fish.

The size of prey listed in Table 2 does not necessarily indicate that these fish are the largest consumed by the seal. Seal generally swallow smaller fish and squid whole below the surface whereas larger fish are brought to the surface and broken into smaller pieces by grasping them with their teeth and shaking them violently from side to side. The largest fish we have seen taken by a seal was a king-of-the-salmon (length 170 cm) which we took away from the animal as it attempted to break the fish into smaller pieces at the surface.

[4]William Gilmartin, Naval Ocean Systems, San Diego, Calif., pers. commun. 1978.

Conclusions

The Pacific white-sided dolphin and the Dall's porpoise feed primarily on small schooling fishes and cephalopods. They, like the northern fur seal, are opportunistic feeders, preying on available species, including some that are commercially important such as salmon, anchovy, jack mackerel, and *Loligo opalescens*. Meaningful estimates of the dolphin and porpoise populations are unavailable, and too few stomachs have been examined to make any estimate of the percentage of commercially important fishes included in the diet.

Regardless of the time of day collected, stomachs may contain undigested fish indicative of recent feeding. Based on stomach content volume and time of collection, large stomach volumes were most often observed in animals collected before 1000 h in the morning, indicating that most feeding is done at night or in the morning.

Northern fur seal tend to congregate in areas of abundant food supply and usually feed at night, probably because most prey species rise toward the surface after dark and are more readily available (Fiscus et al. 1964). Food species consumed by the seal vary by area, but the important food in the diet of this mammal in a given area, based on percentage of stomach content volume, generally does not change—only ranking by volume changes. The animals collected on the continental shelf appear to feed on fishes, whereas those taken beyond the shelf feed primarily on squids.

Acknowledgments

The authors wish to thank John Fitch, California Department of Fish and Game, for identification of fish otoliths from the stomachs of two dolphins; Eric Hochberg, Curator of Invertebrate Zoology, Santa Barbara Museum of Natural History, for identification of the pelagic octopus, *Ocythoe tuberculata*, beaks; and Dale Rice, Northwest and Alaska Fisheries Center, NMFS, NOAA, for his review of the manuscript.

Literature Cited

AMERICAN SOCIETY OF MAMMALOGISTS, COMMITTEE ON MARINE MAMMALS.
1961. Standardized methods for measuring and recording data on the smaller cetaceans. J. Mammal. 42:471-476.
1967. Standard measurements of seals. J. Mammal. 48:459-462.

BAILEY, R. M., J. E. FITCH, E. S. HERALD, E. A. LACHNER, C. C. LINDSEY, C. R. ROBINS, AND W. B. SCOTT.
1970. A list of common and scientific names of fishes from the United States and Canada. 3d ed. Am. Fish. Soc., Spec. Publ. 6, 149 p.

BEST, E. A.
1963. Contribution to the biology of the Pacific hake, *Merluccius productus* (Ayres). Calif. Coop. Oceanic Fish. Invest. Rep. 9:51-56.

BROWN, D. H., AND K. S. NORRIS.
1956. Observations of captive and wild cetaceans. J. Mammal. 37:311-326.

COWAN, I. MCT.
1944. The Dall porpoise, *Phocoenoides dalli* (True), of the northern Pacific Ocean. J. Mammal. 25:295-306.

FISCUS, C. H.
1978. Northern fur seal. *In* D. Haley (editor), Marine mammals of eastern North Pacific and Arctic waters, p. 152-159. Pac. Search Press, Seattle, Wash.
1979. Interactions of marine mammals and Pacific hake. Mar. Fish. Rev. 41(10):1-9.

FISCUS, C. H., G. A. BAINES, AND F. WILKE.
1964. Pelagic fur seal investigations, Alaska waters, 1962. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 475, 59 p.

FISCUS, C. H., AND K. NIGGOL.
1965. Observations of cetaceans off California, Oregon, and Washington. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 498, 27 p.

FITCH, J. E., AND R. L. BROWNELL, JR.
1968. Fish otoliths in cetacean stomachs and their importance in interpreting feeding habits. J. Fish. Res. Board Can. 25:2561-2574.

FITCH, J. E., AND R. J. LAVENBERG.
1971. Marine food and game fishes of California. Univ. Calif. Press, Berkeley, 179 p.

HIGGINS, E.
1919. Porpoise captured. Calif. Fish Game 5:157.

HOTTA, H., H. MAKO, K. OKADA, AND U. YAMADA.
1969. On the stomach contents of dolphins and porpoises off Kyushu. [In Jpn., Engl. summ.] Bull. Seikai Reg. Fish. Res. Lab. 37:71-85.

HOUCK, W. J.
1961. Notes on the Pacific striped porpoise. J. Mammal. 42:107.

KEYES, M. C.
1968. The nutrition of pinnipeds. *In* R. J. Harrison (editor), The behavior and physiology of pinnipeds, p. 359-395. Appleton-Century-Crofts, N.Y.

KOGA, S.
1969. On the Dall's porpoise, *Phocoenoides dalli* (True), caught by the Japanese salmon fishing gill-net in the northern waters of the Asian side. Shimonoseki Univ. Fish., Contrib. 585:53-63.

KOOYMAN, G. L., R. L. GENTRY, AND D. L. URQUHART.
1976. Northern fur seal diving behavior: A new approach to its study. Science (Wash., D.C.) 193:411-412.

LANDER, R., AND H. KAJIMURA.
1976. Status of northern fur seals. Food Agric. Organ. U.N., Adv. Comm. Mar. Resour. Res. FAO ACMRR/MM/SC/34, 50 p.

LOEB, V. J.
1972. A study of the distribution and feeding habits of the Dall porpoise in Monterey Bay, California. M.S. Thesis, San Jose State College, San Jose, Calif., 62 p.

MARINE MAMMAL BIOLOGICAL LABORATORY.
1969. Fur seal investigations, 1966. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 584, 123 p.
1970. Fur seal investigations, 1968. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-617, 125 p.

MIZUE, K., AND K. YOSHIDA.
1965. On the porpoises caught by the salmon fishing gill-net in Bering Sea and the North Pacific Ocean. [In Jpn., Engl. summ.] Fac. Fish., Nagasaki Univ., Bull. 19:1-36.

MIZUE, K., K. YOSHIDA, AND A. TAKEMURA.
1966. On the ecology of the Dall's porpoise in Bering Sea and the North Pacific Ocean. [In Jpn., Engl. summ.] Fac. Fish., Nagasaki Univ., Bull. 21:1-21.

NATIONAL MARINE FISHERIES SERVICE.
1978. The Marine Mammal Protection Act of 1972; Annual Report: April 1, 1977 to March 31, 1978. U.S. Dep. Commer., Natl. Oceanic Atmos. Adm., Natl. Mar. Fish. Serv., Wash., D.C., 183 p.

NORRIS, K. S., AND J. H. PRESCOTT.
1961. Observations on Pacific cetaceans of Californian and Mexican waters. Univ. Calif., Publ. Zool. 63:291-401.

PEARCY, W. G., E. E. KRYGIER, R. MESECAR, AND F. RAMSEY.
1977. Vertical distribution and migration of oceanic micronekton off Oregon. Deep-Sea Res. 24:223-245.

RIDGWAY, S. H.
1966. Dall porpoise, *Phocoenoides dalli* (True): Observations in captivity and at sea. Nor. Hvalfangst-Tidende 55:97-110.
1972. Homeostasis in the aquatic environment. *In* S. H. Ridgway (editor), Mammals of the sea, biology and medicine, p. 590-747. Charles C. Thomas Publ., Springfield, Ill.

RIDGWAY, S. H., AND D. G. JOHNSTON.
1966. Blood oxygen and ecology of porpoises of three genera. Science (Wash., D.C.) 151:456-458.

ROPER, C. F. E., AND R. E. YOUNG.
1975. Vertical distribution of pelagic cephalopods. Smithson. Contrib. Zool. 209, 51 p.

SCHEFFER, V. B.
1953. Measurements and stomach contents of eleven delphinids from the northeast Pacific. Murrelet 34:27-30.

SERGEANT, D. E.
1969. Feeding rates of cetacea. Fiskeridir. Skr. Ser. Havunders. 15:246-258.

WILKE, F., AND A. J. NICHOLSON.
1958. Food of porpoises in waters off Japan. J. Mammal. 39:441-443.

WILKE, F., T. TANIWAKI, AND N. KURODA.
1953. *Phocoenoides* and *Lagenorhynchus* in Japan, with notes on hunting. J. Mammal. 34:488-497.

YOUNG, R. E.
1972. The systematics and areal distribution of pelagic cephalopods from the seas off Southern California. Smithson. Contrib. Zool. 97, 159 p.

RICHARD K. STROUD

Northwest and Alaska Fisheries Center
National Marine Fisheries Service, NOAA
7600 Sand Point Way NE., Seattle, WA 98115
Present address: *Department of Veterinary Medicine*
Oregon State University
Corvallis, OR 97331

CLIFFORD H. FISCUS
HIROSHI KAJIMURA

Northwest and Alaska Fisheries Center
National Marine Fisheries Service, NOAA
7600 Sand Point Way NE., Seattle, WA 98115

SPAWN AND LARVAE OF THE PACIFIC SANDFISH, *TRICHODON TRICHODON*

Little is known about the biology of the Pacific sandfish, *Trichodon trichodon*, other than that the adults are characteristic of inshore, sand-gravel communities (Isakson et al. 1971); they occur from San Francisco, Calif., to Kamchatka, USSR (Hart 1973); and they burrow into a sandy substrate (Clemens and Wilby 1961). Clemens and Wilby reported that a mature female taken on Long Beach, Vancouver Island, Canada, extruded mature eggs (upon disturbance) in February.

The first discovery of natural spawn of *T. trichodon* and subsequent rearing of larvae through metamorphosis at the Vancouver Public Aquarium has provided information about the reproduction and early life history of this species. In addition to life history notes, this paper presents a description of larvae of *T. trichodon*.

Methods

A portion of an egg mass was collected at lat. 48°56′ N, long. 125°43′ W, 16 km southeast of Long Beach, Vancouver Island, on 12 June 1976 and transported in a plastic bag with oxygen and seawater to the Vancouver Aquarium, where it was incubated in an aerated aquarium with seawater (25-29‰, 8°-13° C) provided at an inflow rate exceeding 100 tank volumes/d. The seawater temperature changed seasonally with changes in average ambient seawater surface temperatures, so that the salinity/temperature regime was comparable with that which the eggs would have encountered intertidally. The eggs were fixed in a bag of nylon mesh in front of the inlet pipe. In October, December, and January, embryos were excised from a few of the eggs to determine whether development was continuing. About once per month egg membranes were scrubbed with a bottle brush to remove diatom growth.

As they hatched the larvae were collected with a beaker and transferred to a 1,000 l rearing tank (ca. 1 m depth × 1 m in diameter) with seawater (25-27‰, 10°-12° C) inflow at a rate exceeding one tank volume per day and a light cycle of 14 h light and 10 h dark, including simulated twilight periods. Larvae were provided brine shrimp, *Artemia salina*, nauplii daily in excess quantities. Debris was siphoned from the tank bottom daily and examined for dead fish larvae. Juveniles were placed in a tank with a sand bottom and flow-through seawater and were fed frozen euphausiids and frozen brine shrimp.

At various ages specimens were preserved in 3% Formalin[1] in seawater, with borax and Ionol. Freshly killed specimens were measured to the nearest 0.5 mm standard length (SL), then measured again 1 yr after preservation, to determine shrinkage. Line drawings, morphometric data, and meristic characters were based on preserved specimens.

Life History Notes

The egg mass was found in a surge channel on a rocky shoreline between 0.6 and 1.0 m tide levels. The mass was visually estimated to have about 1,000 eggs, was irregularly shaped, and adhered firmly to the rock surface.

Adults of this species are known to inhabit sandy beaches, whereas the egg mass is suited only to rocky substrate to which it can adhere. Presuming an incubation period of about 1 yr as discussed below, most plant substrates would be too ephemeral for an egg deposition site and bedrock on sand beaches could be covered by seasonal shifting of sand. Rocky shoreline removed from sandy areas would therefore provide the most stable substrate for the adhesive eggs. The precise location on the wall of a fully exposed surge channel might provide a refuge from egg predation as well as high flow velocities for gas exchange. The rocky intertidal area in which this egg mass occurred is located 8 km from the nearest sandy intertidal area. Thus, a limited spawning movement along the shore must occur.

[1]Reference to trade names does not imply endorsement by the Vancouver Aquarium or by the National Marine Fisheries Service, NOAA.

The *T. trichodon* eggs were amber colored and large in size (3.52 mm in diameter ±0.10 SE, n = 17 eggs), and slightly flattened at points of attachment. About 25% of the collected eggs were dead at the time they were taken. When collected the embryos had developed both melanic choroid pigment and guanine iris pigment on the eyes.

Considering the state of development of these embryos, it was expected that these eggs would mature and hatch within a month after collection, since benthic egg masses of many northeast Pacific fishes mature to hatching within 1 to 3 mo after fertilization (pers. obs. on 28 species). The *T. trichodon* eggs, however, continued to develop for over 8 mo after they were collected, then all hatched within a 24-h period.

As a basis for comparison, wolf-eel, *Anarrhichthys ocellatus*, eggs are large (ca. 5 mm in diameter) and have a relatively long incubation of 3 mo at 10°-12° C (pers. obs. on captive spawn). At 1 mo after fertilization (one-third of incubation period), *A. ocellatus* embryos reach a developmental state comparable with that of the *T. trichodon* at the time of the collection, with pigmented eyes on an embryo still many times smaller than the yolk sac. Assuming comparability in relative rates of development, a full incubation period of 12 mo could therefore be calculated for the *T. trichodon*. An incubation period of 1 yr would indicate February as the time of spawning, which coincides with the finding of a ripe female in February in the same area of Vancouver Island (Clemens and Wilby 1961).

About 90% of the hatch occurred within 4 h, in late afternoon, the remainder the next morning. The *T. trichodon* eggs had not been handled for 2 wk prior to hatching and no other fish eggs had hatched in the incubation tank for a week prior to this hatch, so it appears unlikely that this abrupt hatch was unnaturally stimulated. Only a few egg mortalities occurred during the incubation period in the laboratory; this low egg mortality, together with the occurrence of an abrupt and fully viable hatch, indicates that the observed incubation period was normal for this species, as an abnormal incubation should adversely affect viability. Although incubation periods of about 1 yr have been reported for an unrelated fish species, *Agonus cataphractus* (see Breder and Rosen 1966 for review), such prolonged incubation is evidently rare.

The larvae were reared in the laboratory from hatching through metamorphosis with no mortalities (maximum age 29 mo, 137 mm SL). Larvae hatched on 15 and 16 February 1977 at 14.5 mm SL (16 mm TL) and grew to 40-43 mm SL (45-50 mm TL) in 70 d, by which time the fish resembled small adults. Allometric growth in the deeping and lateral compression of the ventral body continued to about 50 mm SL, along with upturning of the jaw and development of fringed lips, as shall be discussed in the following section.

Immediately upon hatching the larvae swam to the water surface and began schooling at the surface in a two-dimensional array (one-fish deep). This neustonic schooling behavior shifted to a pattern of subsurface schooling (three-dimensional schools, usually within 10 cm of the surface) at about 48 h after hatching. At this time, feeding was first noted. By 72 h after hatching, about half the larvae had food in the guts within 4 h of the daily food introduction; about 80% had full guts after introduction of food on day 4 (96 h). Schooling behavior was characteristic of the entire period of larval development; these schooling tendencies decreased progressively during metamorphosis (from about 30 to 50 mm SL) and the juveniles did not show true schooling behavior in the confines of aquaria.

The larval *T. trichodon* were rapid swimmers. Alexander (1967) mentioned 10 body lengths/s as a maximum burst speed for teleosts of any size and 3-5 body lengths/s as a maximum sustained speed (maintained for at least several minutes). Although no effort was made to determine precisely the cruising speed of larval *T. trichodon*, observations of the distance traversed in 5 s intervals revealed a cruising speed of about 10 body lengths/s and always over 5 body lengths/s. This rapid swimming occurred abruptly upon hatching, before the onset of feeding. Synchronized hatching, the abrupt onset of schooling, and rapid swimming may have evolved as mechanisms for larvae to escape the physical dangers of the wave-swept incubation site.

Trichodon trichodon first burrowed into sand as metamorphosed juveniles of 50-60 mm SL. They burrowed by simultaneously undulating the body laterally while fanning the pectoral fins upward and forward, so that the body sank downward and backward into the sand. The eyes and nostrils usually remained exposed above the sand, although the entire body could be buried. Burrowing did not occur until fleshy fringes had developed on the jaws. The fringed lips may permit water to be inhaled without allowing sand to enter the buccal cavity. The allometric growth prior to inital bur-

rowing may indicate a functional role of the deep, narrow form of the ventral part of the body in burrowing.

Larval Development

Morphometric and meristic features of an excised embryo (2 wk prior to hatching) and larvae of nine posthatching ages are presented in Table 1. The outstanding feature of the late embryo was the presence of caudal fin rays and a flexing notocord with the posterior margins of the hypural plates about 45° to the horizontal body axis. This precocious development of the caudal fin remained a diagnostic character throughout the larval period and probably contributed to the rapid swimming speeds discussed earlier.

The late embryo and the newly hatched larvae have a large oil droplet positioned anteriorly in the yolk. The abdomen has about 40 melanophores radiating from the dorsal gut surface. In addition to the features detailed in Table 1, these early ages have a few external melanophores in the nasal region, lower jaw angle, cranial region (7-10), and anterior mandibles (Figure 1). There is also an internal melanophore anterior to each otic capsule and, in fresh material, about 30 xanthophores over the cranium. Three preopercular spines are present as are the pectoral fin rays.

By 9 d hatching age, the posterior margins of the hypural plates are approaching a vertical orientation and have an increased number of melanophores, while the caudal and pectoral fin rays have increased in length. There is a row of 4 or 5 small melanophores along each side of the anterior insertion of the dorsal fin fold and an internal row of about 24 melanophores along the notocord (less clearly visible than external pigment, therefore not illustrated). Eight small melanophores have appeared in the cranial region, clustered among six larger ones, previously developed. A single melanophore has appeared on the ventral midline of the lower jaw (not visible in side view). Rows of melanophores have also appeared along the anterior end of the mandibles and horizontally on the dorsal portion of the operculum. Snout melanophores become prominent by this stage, as do teeth on the lower jaw. These teeth are easily visible at this stage, becoming progressively reduced until, at 25 d hatching age, they are no longer noticeable.

The 18-d specimen has vertical posterior margins on the hypural plates, a forked caudal fin, and

TABLE 1.—Count and morphometric data during early development of *Trichodon trichodon*. Fresh length, immediately after killing; preserved length, 1 yr later.

Hatched age (d)	Fresh length (mm SL)	Preserved length (mm SL)	SL percent shrinkage	Preserved snout-anus length (mm)	Ratio snout-anus ÷ SL	Preserved body depth (mm)	Ratio body depth SL	Myomeres		Fin ray counts				Melanophore count	
								Preanal	Postanal	D-1	D-2	Anal	Pectoral	Pelvic	PVM[1]	Hypural
Embryo	—	11.0	—	—	—	—	—	12	36	0	0	0	—	0	16	3
0	14.5	13.0	10.3	4.5	0.35	2.5	0.19	12	38	0	0	0	—	0	18	3
0	14.5	13.0	10.3	4.5	0.35	2.7	0.21	12	38	0	0	0	—	0	16	1
0	14.5	13.0	10.3	4.5	0.35	2.7	0.21	12	40	0	0	0	—	0	20	2
9	—	14.5	—	5.0	0.34	3.0	0.21	12	37	0	0	0	—	0	16	4
18	19.5	17.2	11.8	7.0	0.41	3.3	0.19	12	37	0	0	0	21	0	20	6
25	21.0	20.0	4.8	8.7	0.43	4.2	0.21	14	34	VIII	15	28	21	0	18	Bands
29	24.5	22.0	6.1	9.3	0.42	5.0	0.23	15	34	X	19	27	21	0	19 - 19	Bands
35	27.5	27.0	1.8	12.0	0.44	5.5	0.20	14	32	XII	18	1.28	21	3	19 - 21	Bands
43	29.0	28.0	3.4	12.7	0.45	6.8	0.24	15	34	XIII	18	1.28	21	1.3	25	Brackets
56	31.5	30.0	4.8	14.0	0.47	7.0	0.23	13	35	XIV	19	1.29	23	1.5	19	Brackets
56	32.5	32.0	1.5	15.0	0.47	7.0	0.22	14	36	XIII	18	1.28	21	1.5	20	Brackets
70	40.0	38.0	5.0	18.0	0.47	9.3	0.24	14	36	XIV	1.19	1.29	22	1.5	15	Brackets
70	43.0	40.5	5.8	20.5	0.51	11.0	0.27	14	34	XIV	1.17	1.27	22	1.5	12	Brackets

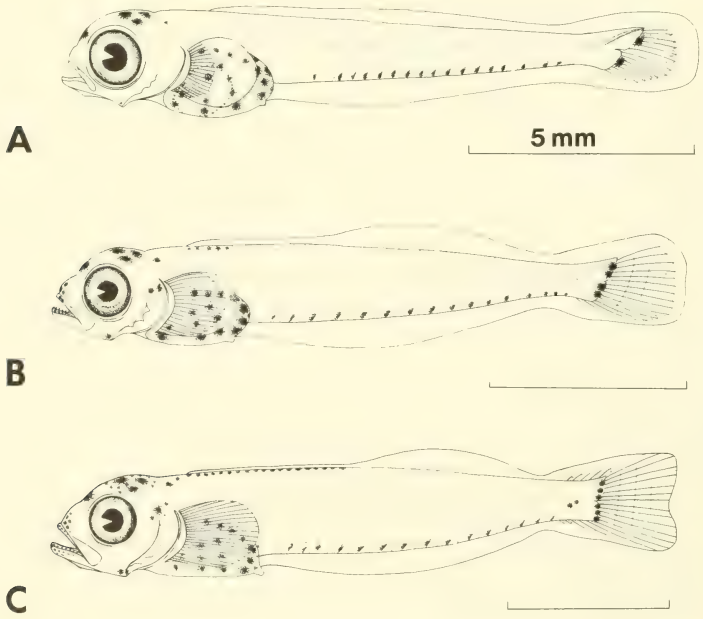
[1]Postanal ventral midline melanophores versus hypural melanophores
[2]Internal and superficial melanophore counts

secondary caudal fin rays. Melanophores are more numerous along the insertion of the dorsal fin fold (18-19 each side), internally along the notocord (27; vague, not illustrated), along the ventral midline of the lower jaw (10), in the cranial region (7 large, 23 small), and on the posterior margin of the hypurals (6). Melanophores appear larger and more dense on the dorsal gut surface as well. Two melanophores are present laterally at the angle of the notocord and 10 melanophores are visible on the principal caudal rays. Pectoral fin ray development is complete (21 rays) and four preopercular spines are evident.

By 25 d hatching age the melanic pigmentation of the dorsal body surface, jaw, and snout has proliferated considerably, while dorsal and anal fin ray development has started (Table 1) and pelvic fin buds are visible. Paired rows of 38 large melanophores occur on the dorsal body along the entire length of the dorsal fin. Cranial melanophores appear as a pair of dense patches (one on each side) with a third median patch on the nape region. The postanal ventral midline melanophores appear more internal than at younger ages. A new row of superficial melanophores has appeared on the mediolateral trunk musculature (posterior half of body), while the angle of the notocord is overlaid by an angular "bracket" of small melanophores, the dorsal leg of which continues anteriorly as a faint internal row dorsal to the notocord. The melanophores at the posterior margin of the hypurals form continuous vertical bands on each plate. Finally, a fifth preopercular spine is becoming visible ventrally.

The 29-d specimen (not illustrated in Figure 1) is marked by the appearance of a ring of small melanophores around each eye, the development of both internal and superficial ventral midline melanophores (Table 1) and doubled rows of melanophores along each side of the dorsal fin base on the anterior half of the body. Cranial and dorsal gut melanophores have continued to become more dense and the pelvic fins are formed, without elements.

At 35 d hatching age, melanophores are on the dorsal margin and dorsal insertion of the pectoral fin and melanophores are arrayed in double or triple rows on each side of the dorsal fin bases



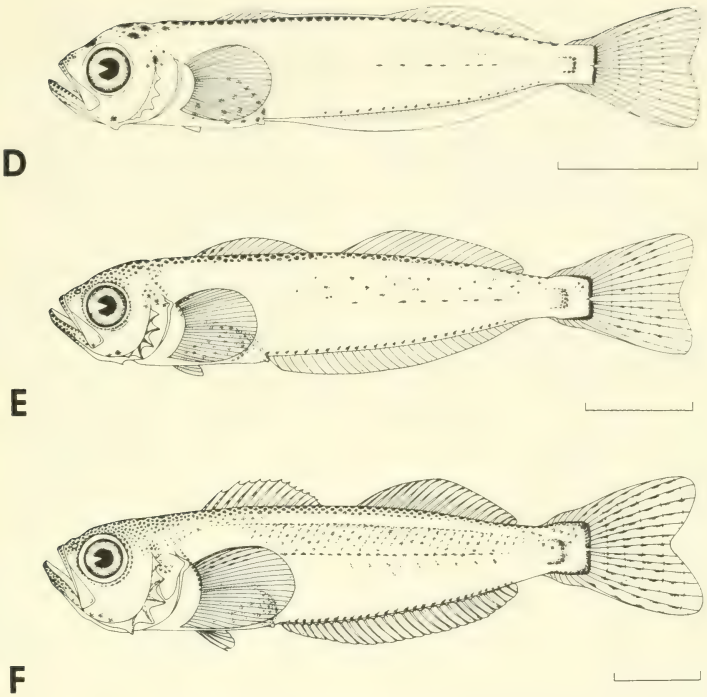


FIGURE 1.—Larvae and early juveniles of *Trichodon trichodon* (preserved lengths). A. 0 d, 13 mm SL; B. 9 d, 14.5 mm SL; C. 18 d, 17.2 mm SL; D. 25 d, 20 mm SL; E. 35 d, 27 mm SL; F. 56 d, 32 mm SL.

posteriorly to the middle of the second dorsal, continuing as single rows across the peduncle. Melanophores are on the first three elements of the first dorsal fin. On the lower jaw, melanin has extended posteriorly to the juncture with the maxillaries. A patch of melanophores has developed on the dorsal preoperculum. About 26 scattered melanophores appear dorsolaterally on the trunk musculature, above the mediolateral row, and melanophores occur closely spaced, lining the edges of principal caudal rays. The melanophores on the hypural margins have spread anteriorly along the insertion of the secondary caudal rays. Allometric growth at this age includes an increase in the relative snout-anus length (Table 1) and a slight upturning of the jaw.

The 43-d specimen (not illustrated) exhibits more regular arrays of the most recently developed melanophore patterns: the mediolateral row consists of 33 melanophores, the dorsolateral melanophores now form broken rows along the margins of myomeres, and the caudal rays are lined with rows of melanophores. By this age, gut melanophores appear internal rather than external. Only superficial ventral midline melanophores (25) are visible.

The 56-d specimen is easily recognized as a young sandfish. The entire snout, jaw, cranium, and nape regions are densely covered with melanophores, continuous with rows along the dorsal fin bases. The upper pectoral fin rays are lined with melanophores, as are the spines on the anterior half of the first dorsal fin. More melanophores have appeared over the caudal peduncle. All fins are completely formed by this stage and the five preopercular spines appear to radiate from a centrum.

By 70 d hatching age the body proportions re-

semble those of the adult. Hart (1973) listed body depth as 0.28 SL for adults, which compares with 0.27 SL for the 70-d specimen (Table 1). The snout-anus length has reached the adult proportion of 0.5 SL (Hart 1973) by this stage. The jaw angle and eye position have not attained adult character by 70 d, however, and the fringed lips and elongate nostrils of the adult are not evident. These features are present by the time burrowing behavior first appears at sizes of about 55-60 mm SL (165 d).

Discussion

Larvae of *T. trichodon* are distinct and easily identified. Myomere counts alone would separate *T. trichodon* from other elongate larvae in the northeastern Pacific. As mentioned, the early development of the caudal fin is a distinguishing character of all early larval stages of *T. trichodon*. The newly hatched yolk-sac larva has a flexed notocord and developing caudal rays. The caudal fin is forked and has secondary rays developing prior to the development of elements of other median fins.

The melanophore patterns developed in gradual stages with little variation among the individuals from this particular hatch. The most distinctive melanophores are perhaps those in the caudal region, on the hypural margins, and at the notocord bend. The overall melanophore patterns for each stage could probably be used as a basis for diagnosis, certainly when taken together with the morphometry and fin development patterns.

The preopercular spines are present at hatching and seem unique among sympatric elongate larvae. The stellate arrangement of these spines in the later development stages is unique.

Altogether, there appears to be little chance for misidentification of this species in the northeast Pacific region. This is of interest in light of the absence of these larvae from records of ichthyoplankton surveys in this region (e.g., Richardson and Pearcy 1977). In the Gulf of Alaska, where *T. trichodon* is an abundant inshore fish species, only one larva has been taken by plankton nets in an extensive ichthyoplankton survey (Kendall[2]). The only other northeast Pacific larvae, of which I am aware, with such high-speed schooling in a laboratory situation are those of *Ascelichthys rhodorus* (pers. obs.), which also do not appear in plankton nets (Richardson and Pearcy 1977). Although this behavior may enhance evasive capabilities in areas sampled for plankton, a further possibility is that this behavior may enable larvae to inhabit the extreme nearshore, which is usually not included in regular plankton surveys.

[2]Arthur W. Kendall, Jr., Fishery Biologist, Northwest and Alaska Fisheries Center, NMFS, NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112, pers. commun. August 1979.

Acknowledgments

I thank Murray Newman, Director of the Vancouver Aquarium, for encouraging and supporting this study, and Arthur W. Kendall, Northwest and Alaska Fisheries Center, NMFS, NOAA, for critical review of the text. James Cave collected the eggs and Robin Ade drew the illustrations.

Literature Cited

ALEXANDER, R.
1967. Functional design in fishes. Hutchinson, Lond., 160 p.

BREDER, C. M., JR., AND D. E. ROSEN.
1966. Modes of reproduction in fishes. Natural History Press, Garden City, N.Y., 941 p.

CLEMENS, W. A., AND G. V. WILBY.
1961. Fishes of the Pacific coast of Canada. Fish. Res. Board Can., Bull. 68, 443 p.

HART, J. L.
1973. Pacific fishes of Canada. Fish. Res. Board Can., Bull. 180, 740 p.

ISAKSON, J. S., C. A. SIMENSTAD, AND R. L. BURGNER.
1971. Fish communities and food chains in the Amchitka area. BioScience 21:666-670.

RICHARDSON, S. L., AND W. G. PEARCY.
1977. Coastal and oceanic fish larvae in an area of upwelling off Yaquina Bay, Oregon. Fish. Bull., U.S. 75:125-145.

JEFFREY B. MARLIAVE

Vancouver Public Aquarium
P.O. Box 3232
Vancouver, B.C. V6B 3X8 Canada

A RADIOLOGIC METHOD FOR EXAMINATION OF THE GASTROINTESTINAL TRACT IN THE ATLANTIC RIDLEY, *LEPIDOCHELYS KEMPI*, AND LOGGERHEAD, *CARETTA CARETTA*, MARINE TURTLES[1,2]

In the past 2 yr the National Marine Fisheries Service of the U.S. Department of Commerce has been raising hatchlings of the Atlantic ridley, *Lepidochelys kempi*, and loggerhead, *Caretta caretta*, marine turtles. These are classified as endangered and threatened species under the U.S. Endangered Species Act of 1973 (U.S. Fish and Wildlife Service 1977, 1978). The rearing activity was undertaken to provide a better understanding of the early life histories of those species.

Of immediate concern was the evaluation and treatment of skin, gastrointestinal, lung, and systemic diseases, which emerged rapidly in the captive turtles. Radiologic examination was sought as a possible diagnostic modality for various problems. To this end we have attempted to develop radiologic techniques for the study of normal and diseased animals.

In this paper we report on the use of barium sulfate contrast agent in studying the gastrointestinal (GI) tract of normal turtles and propose its use as an aid in the diagnosis of turtle GI diseases.

Methods

The GI tracts of two loggerhead and two ridley turtles, between the ages of 4 and 10 mo, were examined by means of commercially available 44% (wt/wt) aqueous barium sulfate suspension.[3] Similar suspensions are frequently used in the examination of the GI tract of humans (Margulis 1973; Miller 1973).

Preparation of the GI tract was accomplished by not feeding the animals for 2 d and then giving 0.5 ml of X-Prep, a commercial laxative of extract of senna fruit (Gray Pharmaceutical Company, Norwalk, Conn.), on the day prior to the examination. Next, the esophagus was intubated using a plastic umbilical artery catheter (Argyle, Cat. No. 8888-160-226, Sherwood Medical Co., St. Louis, Mo.) measuring 5 mm in circumference. The intubation of the ridley turtle's esophagus proved more difficult than the loggerhead's as they resisted passage of the catheter through the oropharynx. Therefore, a dose of 0.25 mg of succinylcholine chloride[4] was given subcutaneously in the neck to effect partial skeletal muscle paralysis. Paralysis was adequate in 4 or 5 min, rapidly diminished, and was nearly undetectable in 20 min. (No untoward side effects occurred.) Also, a plastic hollow guide (4 mm in diameter) was placed in the oropharynx and upper esophagus through which the umbilical artery catheter was threaded into the esophagus and stomach. Both the hollow guide and catheter were lubricated with small amounts of surgical lubricant. The placement of the catheter tip in the stomach and injection of approximately 5 ml of contrast material were done under fluoroscopic control. Radiographic films were then exposed using either the phototimed fluoroscopic filming device or manual techniques utilizing standard radiographic equipment, film, and film cassettes. The fluoroscopic unit, radiographic equipment, radiographic film, and film cassettes which were used are of standard medical grade and are available in most radiology departments. Serial filming consisting of fluoroscopic spot films, made in various degrees of obliquity and standard medical radiographic film[5] in cassettes (Halsey Rigidform, Halsey X-Ray Products, Brooklyn, N.Y.) equipped with par speed intensifying screens (Radelin TA-3, GAF Corp., Brooklyn, N.Y.), and industrial grade film[6] in cardboard cassettes made in the dorsoventral (DV) position were done on the day of the examination. For the following 2 d DV par speed medical films or industrial grade films were made on each consecutive day. Thereafter, DV films were exposed every other day for 4 d. Radiographic technique and film types are given in Table 1.

Radiation exposure using industrial film exposed at 60 kV peak and 400 mAs and par speed medical film exposed at 50 kV peak and 10 mAs with a target film distance of approximately 100 cm was 0.98 and 0.14 Roentgen/exposure, respectively. These measurements were obtained using a 0.6 cm^3 Baldwin-Farmer air ionization chamber

[1]The investigations involving the Atlantic ridley turtle were conducted under Permit No. PRT 2-1770 (U.S. Federal Fish and Wildlife Service), permits 1978-ABC-IV-0751, No. 27611-8786, and 1979-ABC-IV-1258, Exp. 4287 (Mexican Government).

[2]Contribution Number 81-1G, Southeast Fisheries Center Galveston Laboratory, National Marine Fisheries Service, NOAA.

[3]E-Z-EM Company, Cat. No. 750, Westbury, N.Y. Reference to trade names or commercial companies does not imply endorsement by the National Marine Fisheries, NOAA.

[4]Succinylcholine HCl injection U.S.P., Oraganon, Inc., West Orange, N.J.

[5]Kodak XRP-1, Eastman Kodak Co., Rochester, N.Y.

[6]Kodak RP/M, Eastman Kodak Co., Rochester, N.Y.

TABLE 1.—Radiographic technique for turtle examinations.

Weight (g)	Carapace length (cm)	Turtle position	Voltage (kV)	Current (mAs)	Tube-film distance (cm)	Film type
400	15.0	DV[1]	60	400	100	Industrial
300	12.5	DV	50-55	300-360	100	Industrial
350	13.5	DV	50	40	100	Industrial
400	13.0	DV	50	10	100	Medical
300-400	13-15	Variable	55-60	Phototimed (fluoroscopy unit)	—	Medical

[1]DV = Dorsoventral projection.

(Nuclear Enterprises, Inc., San Carlos, Calif.) on an electrometer[7] at 300 V collection potential.

Results

Adequate clearing of food residue was obtained after the subjects were prepared in the manner described in Methods. The experimental animals were quite small (0.3-0.4 kg) and good resolution and detail are a necessity if mucosal detail is to be adequately examined and appraised. Excellent detail of the esophagus, stomach, and small intestinal mucosa was obtained by using industrial grade film while adequate detail was obtained on par speed medical film. The radiologic anatomy of the esophagus, stomach, and small intestine correlated well with the findings noted at gross necropsy of turtles of similar age and size that had

[7]Model 602 Electrometer, Keithley Co., Cleveland, Ohio.

FIGURE 1.—Dorsoventral view of a 15 cm carapace length, 400 g, 8-mo-old loggerhead turtle made on the second day after barium instillation. Industrial grade film was used for this exposure. 1—stomach, 2—proximal small bowel, 3—tracheal air shadow, 4—lungs. The arrowheads demonstrate the longitudinal mucosal pattern in the proximal small bowel (1.8×).

died of various causes. Figure 1 shows the relatively smooth mucosa of the stomach which has been distended with barium. The smooth longitudinal folds of the proximal small bowel are also easily identified. Also in Figure 1 just to the left of the tracheal air shadow (3) and superimposed over the cervical vertebrae, a few esophageal papillae are faintly outlined by small amounts of barium. Incidently, injection of contrast directly into the esophagus demonstrated the esophageal papillae and the narrowing in the region of the gastroesophageal junction with greater clarity than in Figure 1. The size and position of the GI structures were also easily assessed. Continued filming over several days demonstrated slow progression of the barium sulfate suspension through the small intestine into the colon. In the colon residual fecal contents mixed with the barium and obscured the mucosal detail somewhat. Transit time was noted to be at least 4 or 5 d from the stomach to the proximal colon in all four animals studied.

Discussion

The radiologic examination of the upper GI tract of marine turtles by using barium sulfate as a contrast material provides a potential tool in the evaluation of various diseases in turtle populations. The radiographic information from these studies should aid in evaluating turtles for partial or complete small bowel obstruction, with associated changes in motility and bowel size, and foreign bodies within the intestinal tract such as parasites or bezoars. Diseases altering the mucosal pattern such as ulceration, gastritis, enteritis, or colitis caused by various infectious or inflammatory processes could be demonstrated. The disease states listed above are frequently demonstrated by similar GI studies performed in humans (Paul and Juhl 1972).

The use of succinylcholine chloride in these animals should be approached with caution. The total dose should be divided and given incrementally over 3-5 min until the desired effect is obtained. The use of a well lubricated plastic hollow guide is recommended prior to the decision to use a paralytic agent.

Radiation exposure was of concern but the calculated doses of 0.98 and 0.14 Roentgen/exposure for industrial and par speed medical film were well below the harmful radiation dose in several species of turtles found by Altland et al. (1951) and Cosgrove (1971). They resemble dosage levels used by Gibbons and Greene (1979), which produced no apparent harm to the freshwater turtles in their study. To reduce radiation exposure during the examination the use of par speed medical film which requires a lower radiation dose is recommended when the clinical situation permits. For instance, intestinal obstruction would require only par speed medical film technique, as demonstration of mucosal detail would be unnecessary when assessment of dilatation of the bowel, stasis of contents, and site of the obstructing process would be primary concerns. In examinations where mucosal detail is desirable such as detection of small ulcerations, industrial film and its attendant higher exposures may become necessary.

Acknowledgments

We appreciate the help, encouragement, and support of M. H. Schreiber, Chairman, Department of Radiology, University of Texas Medical Branch, (UTMB), as well as his comments on preparation of this paper; to Robert Perry, health physicist, Department of Radiology, UTMB, for his assistance in taking and calculating the radiation doses; and to Peggy Seibel, residents' secretary, UTMB, for typing the manuscript.

Literature Cited

ALTLAND, P. D., B. HIGHMAN, AND B. WOOD.
1951. Some effects of x-irradiation on turtles. J. Exp. Zool. 118:1-19.

COSGROVE, G. E.
1971. Reptilian radiobiology. J. Am. Vet. Med. Assoc. 159:1678-1684.

GIBBONS, J. W., AND J. L. GREENE.
1979. X-ray photography: a technique to determine reproductive patterns of freshwater turtles. Herpetologica 35:86-89.

MARGULIS, A. R.
1973. Use of iodinated water-soluble contrast agents in acute gastrointestinal disease. *In* A. R. Margulis and H. J. Burhenne (editors), Alimentary tract roentgenology. Vol. 1, p. 271-280. 2d ed. C. V. Mosby Co., St. Louis, Mo.

MILLER, R. E.
1973. Barium sulfate as a contrast medium. *In* A. R. Margulis and H. J. Burhenne (editors), Alimentary tract roentgenology. Vol. 1, p. 114-126. 2d ed. C. V. Mosby Co., St. Louis, Mo.

PAUL, L. W., AND J. H. JUHL.
1972. The abdomen and gastrointestinal tract. *In* The essentials of roentgen interpretation, p. 411-643. 3d ed. Harper and Row, Hagerstown, Md.

U.S. FISH AND WILDLIFE SERVICE.
1977. A guide to endangered species regulations—The

Endangered Species Act (with attachment: 50 CFR17 (Rev. 8/77), p. 1-16.
1978. The Endangered Species Act—The green loggerhead, and olive (Pacific) ridley sea turtles. T-1, p. 1-3.

G. L. McLELLAN

Department of Radiology
University of Texas Medical Branch
Galveston, TX 77550

J. K. LEONG

Southeast Fisheries Center Galveston Laboratory
National Marine Fisheries Service, NOAA
Galveston, TX 77550

SUMMER FOOD OF PACIFIC COD, *GADUS MACROCEPHALUS*, IN COASTAL WATERS OF SOUTHEASTERN ALASKA

The Pacific cod, *Gadus macrocephalus* Tilesius, is ecologically important in the Gulf of Alaska and may be more extensively utilized in future commercial fishing efforts. Although Pacific cod is one of the most abundant demersal fish in shallower (<200 m depth) waters of the Gulf of Alaska (Alverson et al. 1964; Ronholt et al.[1]), it has not been extensively fished. The total harvest of Pacific cod from the Gulf of Alaska (mostly by foreign fishing fleets) is estimated to be a "small fraction of the maximum sustained yield" and "substantially higher catches" could be supported (North Pacific Fishery Management Council[2]). Because of the recent establishment of the 200-mi United States Fishery Conservation Zone and a concurrent interest in bottomfishing, a domestic fishing industry may develop that could also exploit Pacific cod.

Little research has been done on the Pacific cod in Alaskan waters, especially concerning its foods. Most of the studies on Pacific cod have been conducted by Soviet investigators in the northwestern Pacific Ocean (summarized by Moiseev 1953). Jewett (1978) investigated the diet of Pacific cod near Kodiak Island, Alaska. In this note, I report the foods of Pacific cod in a different region of Alaska, southeastern Alaska.

Methods

Pacific cod were sampled during a cruise conducted by the National Marine Fisheries Service primarily to assess cod resources and evaluate different types of fishing gear used. During a 17-d period in July 1977, 520 Pacific cod stomachs were collected in two regions of southeastern Alaska coastal waters: 17 sites in the Gulf of Alaska between Cape Spencer and Yakutat Bay (outside waters, Figure 1) and 34 sites in protected waters between northern Lynn Canal and Frederick Sound (inside waters, Figure 2). Each site was sampled once.

Pacific cod were caught with traps (360 fish) and gill nets (160 fish) in water 38-176 m deep (Table 1). Most fish were caught in waters <90 m deep. Traps, $0.8 \times 0.8 \times 2.4$ m rectangular structures with tunnel openings, were baited with chopped frozen Pacific herring, *Clupea harengus pallasi*, and set on the bottom. Gill nets, 180 m long, made of 15 cm or 17.5 cm diagonal-stretched-mesh monofilament, were set on the bottom or 0.6 m above the bottom. Both gear were set during daylight hours, fished overnight, and retrieved the

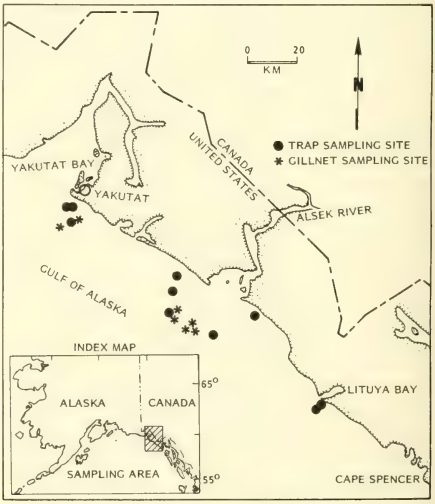


FIGURE 1.—Locations where Pacific cod were sampled in outside waters, southeastern Alaska, July 1977.

[1]Ronholt, L. L., H. H. Shippen, and E. S. Brown. 1978. Demersal fish and shellfish resources of the Gulf of Alaska from Cape Spencer to Unimak Pass 1948-1976 (a historical review). Processed rep., 955 p. Northwest and Alaska Fisheries Center, Natl. Mar. Fish. Serv., NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112.

[2]North Pacific Fishery Management Council. 1978. Fishery management plan for the Gulf of Alaska groundfish fishery during 1978. Unpubl. rep., 220 p. North Pacific Management Council, P.O. Box 3136DT, Anchorage, AK 99510.

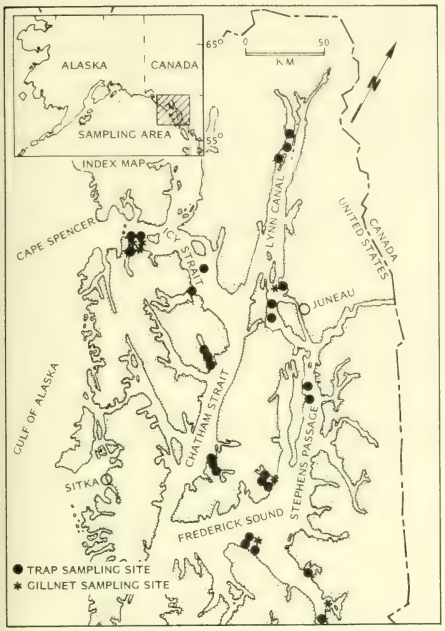


FIGURE 2.—Locations where Pacific cod were sampled in inside waters, southeastern Alaska, July 1977.

TABLE 1.—Summary of samples of Pacific cod caught in gill nets and traps in southeastern Alaskan waters, July 1977. Each site was sampled once.

	Caught in gill nets				Caught in traps			
Area	Sites (no.)	Mean depth (m)	Cod (no.)	Mean length (cm)	Sites (no.)	Mean depth (m)	Cod (no.)	Mean length (cm)
Outside waters	7	149	81	73.9	10	63	135	60.7
Inside waters	7	52	79	72.7	27	70	225	66.0
Both	14	101	160	73.3	37	68	360	64.0

next day. Usually, stomachs were removed from all Pacific cod caught, but random subsamples were taken from a few large catches. Stomachs and regurgitated or undigested food in the esophageal and mouth areas were preserved in Formalin.[3] The sex of each Pacific cod was identified, if possible, and the total length (TL, tip of snout to end of tail) was measured.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Estimated percentage volume of major food categories and frequency of occurrence of each food were determined. The volume of each major food category (i.e., fish, pandalid shrimp) was visually estimated to the nearest 5% for each stomach that arbitrarily appeared to be at least one-fourth full. Foods in stomachs less than one-fourth full were listed only as present and often were slowly digested items, such as fish otoliths or cephalopod beaks in trace amounts. No other allowances were made for stomach fullness. When pooling results, I averaged equally the percentages of each food in all stomachs one-fourth or more full. Visual estimates of the percentage volume of food in each category were generally within 10% of percentages determined by actual measurements of displacement volume. I identified all foods in all stomachs to the lowest taxonomic level possible and calculated the overall frequency of occurrence (expressed as the percentage of stomachs containing the food) of each food.

Volume data on each major food category were analyzed to determine whether relationships existed between foods eaten by Pacific cod and 1) size and sex of Pacific cod, 2) the location at which they were caught (inside waters vs. outside waters), and 3) the type of gear. I arbitrarily separated the Pacific cod into three total length categories to determine whether the different foods eaten were related to size of Pacific cod. The size categories were ≤60 cm, 61-70 cm, and >70 cm. Too few samples were taken at different depths in the same localities to allow analysis of Pacific cod foods by depth.

Results

If data from all areas are combined, regardless of size and sex of Pacific cod and gear type, fish were the most important food of Pacific cod both volumetrically and in frequency of occurrence. Fish accounted for more than 40% of the stomach contents by volume (Table 2) and were in nearly 60% of the stomachs (Table 3). The largest percentage of fish in the stomachs was unidentifiable; however, of the identifiable fish, Pacific herring and walleye pollock, *Theragra chalcogramma*, were eaten most often. Pacific herring ranged from 9 to 25 cm long (mean, 18 cm); walleye pollock, identified by their large and characteristic otoliths, were juveniles and ranged from 10 to 31 cm long (mean, 22 cm). Some of the unidentified fish were probably Pacific herring, pricklebacks

TABLE 2.—Mean estimated percentage volume of foods in stomachs of Pacific cod in southeastern Alaskan waters, July 1977 (stomach fullness one-fourth or greater).

Food item	All areas						Outside waters				Inside waters			
	All fish	All males	All females	<60 cm	61-70 cm	>70 cm	All fish	<60 cm	61-70 cm	>70 cm	All fish	<60 cm	61-70 cm	>70 cm
Fish	42.5	39.4	44.9	17.1	35.4	66.0	35.1	11.9	27.8	61.9	48.0	22.7	40.5	68.7
Crab	26.1	26.5	25.2	38.0	30.3	14.3	44.9	57.7	56.7	21.1	12.1	16.3	12.4	9.8
Shrimp	16.9	21.8	13.9	23.0	20.3	9.1	4.7	6.3	5.0	2.7	26.1	41.6	30.7	13.4
Pandalid	9.7	14.2	7.3	5.6	13.7	7.1	1.0	1.7	.5	.9	16.2	9.9	22.7	11.2
Crangonid	3.5	3.4	3.4	9.6	2.6	1.1	2.6	3.5	2.7	1.5	4.3	16.3	2.6	.9
Hippolytid	2.3	2.9	2.0	4.9	2.5	.6	.3	1.1	1	0	3.8	9.2	4.0	.9
Unidentified	1.4	1.3	1.2	2.9	1.5	.3	.8	0	1.7	.3	1.8	6.2	1.4	.4
Gammarid amphipods	3.5	4.3	3.0	6.9	3.8	1.1	3.8	8.7	2.1	2.3	3.2	4.9	5.0	.2
Cephalopods	3.1	2.2	3.9	2.8	3.6	2.9	1.0	2.9	.5	.2	4.7	2.8	5.6	4.6
Mollusks other than cephalopods	1.7	1.2	1.9	2.7	1.8	1.0	.9	.7	1.5	.9	2.3	4.8	2.0	1.2
Polychaetes	2.2	1.1	2.9	3.0	2.3	1.7	4.2	5.0	3.6	4.3	.7	.8	1.4	0
Other food items and unidentified	4.0	3.5	4.3	6.5	2.5	3.9	5.4	6.8	2.8	6.6	2.9	6.1	2.4	2.1
Cod sampled (no.)	439	163	266	90	193	156	187	47	78	62	252	43	115	94
Mean total length (cm)	67.0	65.2	68.6	53.7	65.6	77.0	65.7	52.2	65.4	77.6	67.7	55.4	65.8	76.6

(Stichaeidae), and eelpouts (Zoarcidae), which are not as distinguishable as walleye pollock and may have been eaten more frequently than the values in Table 3 indicate. Flatfish (Pleuronectidae) were easily recognized and, because few were found, were probably not an important food for Pacific cod in these waters during July.

Crab and shrimp were the next most important foods. The volume of crab in Pacific cod stomachs was greater than the volume of shrimp; however, the frequency of occurrence of shrimp was greater than the frequency of occurrence of crab. Snow crab, *Chionoecetes bairdi*, the crab most often eaten by Pacific cod, were juveniles and ranged from 5 to 42 mm carapace width (mean, 20 mm). As many as 30 snow crabs were found in some stomachs. Dungeness crab, *Cancer magister*, was the only other crab eaten in more than incidental numbers. Pagurids (hermit) and other anomuran crabs were rarely eaten. Pandalid shrimp, particularly *Pandalus tridens* and *P. borealis*, were more frequently eaten than either crangonid or hippolytid shrimp, and all three families of shrimp were often found together in stomachs.

Other invertebrates were found in the Pacific cod stomachs, but their volumes and frequencies were small. Cephalopods were in more than 14% of the stomachs but constituted only 3.1% of the mean volume. Often only the cephalopod's horny beaks were present; however, whole *Octopus* sp. formed the bulk of the stomach contents of a few Pacific cod. Gammarid amphipods were in 14% of the stomachs. Pelecypods, mostly *Nuculana* sp., were infrequently eaten. The large polychaete *Aphrodita* sp. ("sea mouse") was found in some stomachs and composed most of the volume for the polychaetes. Planktonic foods, such as euphausiids or mysids, were rarely found and then, only in trace amounts.

At all locations, the size of the Pacific cod affected the kinds of food eaten (Table 2). Small Pacific cod (≤60 cm) fed mostly on crab and shrimp; only 17% of the estimated volume of their stomach contents was fish. Large Pacific cod (>70 cm long) fed predominately on fish (66% by volume). The diet of intermediate-sized Pacific cod (61-70 cm) was transitional between the diets of the small and large Pacific cod.

Sex of Pacific cod did not appear to be related to the major foods eaten (Table 2). Fifty-nine percent of the Pacific cod were females, 38.7% were males, and 2.3% were of unidentified sex. Females had a mean of 68.6 cm TL; males, 65.2 cm TL. The minor differences that did arise between the foods of each sex can probably be attributed to the greater mean length of females.

Foods of Pacific cod in outside waters were different from foods of those in inside waters (Tables 2, 3). Pacific cod in outside waters ate a larger volume of crabs (mostly juvenile snow crab) than those in inside waters; however, in inside waters, the volume of shrimp (particularly pandalid shrimp) in the stomachs was much higher than in outside waters. These differences in the volume of foods eaten were especially pronounced for small and intermediate-sized Pacific cod. All sizes of Pacific cod ate more fish in the inside waters than in the outside waters. Pacific herring, especially, were heavily consumed in inside waters.

The two gear (gill nets and traps) probably did not significantly bias the results. Comparison of foods in Pacific cod caught by gill nets and foods in

TABLE 3.—Frequency of occurrence of food items ≥1.0% in stomachs of 492 Pacific cod, southeastern Alaskan waters, July 1977 (based only on stomachs containing food).[1]

Food item	Frequency of occurrence (%)		
	All areas	Outside waters	Inside waters
Fishes	58.5	54.2	61.5
Clupea harengus pallasi	9.6	1.0	15.5
Theragra chalcogramma	8.7	8.5	8.9
Stichaeidae	2.8	.5	4.5
Unidentified stichaeids	2.2	.5	3.4
Pleuronectidae	1.8	2.5	1.4
Unidentified pleuronectids	1.0	.5	1.4
Zoarcidae	1.2	.5	1.4
Unidentified	36.4	38.3	35.1
Shrimps	46.5	24.9	61.5
Pandalidae	25.4	7.0	38.1
Pandalus tridens	5.5	4.5	6.2
P. borealis	4.7	0	7.9
P. danae	1.8	0	3.1
P. hypsinotus	1.6	0	2.7
Unidentified pandalids	15.2	1.7	24.1
Crangonidae	18.9	16.9	20.3
Crangon spp.	8.9	6.0	10.7
Argis sp.	1.0	2.0	.3
Unidentified crangonids	9.2	9.0	8.6
Hippolytidae	9.6	1.5	15.1
Unidentified shrimp	7.7	4.5	10.0
Crabs	39.6	62.7	23.7
Brachyuran crabs	32.3	58.2	14.4
Chionoecetes bairdi	26.2	44.8	13.4
Cancer magister	4.1	10.0	0
Hyas lyratus	1.0	1.5	.7
Unidentified brachyurans	2.2	4.0	1.0
Anomuran crabs	3.7	1.0	5.5
Unidentified pagurids	2.8	.5	4.5
Unidentified crabs	2.6	2.5	2.7
Cephalopods	14.4	9.5	17.9
Octopus sp.	4.1	1.5	5.8
Unidentified cephalopods	10.0	7.0	12.0
Gammarid amphipods	14.0	16.4	12.4
Pelecypods	11.4	7.5	14.1
Nuculana sp.	7.5	3.0	10.7
Unidentified pelecypods	3.3	3.0	3.4
Polychaetes	6.5	10.9	3.4
Aphrodita sp.	3.7	8.5	.3
Unidentified polychaetes	2.6	2.5	2.7
Gastropods	3.9	2.5	4.8
Natica sp.	1.2	2.0	.7
Unidentified gastropods	2.2	0	3.8
Algae	3.0	3.0	3.1
Euphausiids	3.0	0	5.1
Isopods	1.6	2.5	.3
Rocinela sp.	1.6	2.5	.3
Mysids	1.0	0	1.7
Unidentified food items	2.6	3.5	2.1

[1]Also present at frequencies <1.0%: Fishes—*Lumpenus maculatus, L. sagitta, Hippoglossoides elassodon, Lepidopsetta bilineata, Lycodes brevipes, L. palaeris, Dasycottus setiger, Coryphaenoides* sp., *Raja* sp. embryo, unidentified fish eggs; shrimps—*Pandalus stenolepis, P. goniurus, P. platyceros*; crabs—*Oregonia gracilis, Lopholithodes* sp., *Labidochirus splendescens*; cephalopods—*Rossia pacifica*; pelecypods—*Siliqua patula, Chlamys rubidus, Serripes groenlandicus*; polychaetes—*Abarenicola* sp.; gastropods—*Lora* sp., *Neptunea* sp.; barnacles—*Lepas* sp., unidentified barnacles; sipunculids; hydroids; ophiuroids; nemerteans; anthozoans; poriferans; foraminifera; unidentified invertebrate eggs.

Pacific cod caught by traps was difficult because the two gear, which tend to catch different sizes of fish, were frequently set at different localities or depths (Table 1; Figures 1, 2). However, when traps and gill nets caught similar-sized fish in the same areas, foods were also similar (see Table 4, Pacific cod 61-70 cm TL in outside waters and >70 cm TL in inside waters). In other cases, locality rather than gear appeared to be the overriding factor determining kinds of food eaten. Of the 24 Pacific cod sampled in the 61-70 cm TL gill net category in inside waters, 15 were taken in Idaho Inlet. There, Pacific herring apparently were so abundant that all sizes of Pacific cod caught in both gill nets and traps fed upon them.

The volume of gammarid amphipods in the stomachs of Pacific cod caught in traps may have been artificially high. Gammarid amphipods were almost exclusively found in Pacific cod caught in traps (Table 4). These amphipods were probably attracted to the baited traps where Pacific cod in the traps fed upon them. In contrast, other invertebrates, such as shrimp or crabs, appeared to be found equally in stomachs of Pacific cod caught in either traps or gill nets.

Discussion

The major foods identified in this study are similar to the major foods of Pacific cod in other regions of the North Pacific Ocean. Walleye pollock and Pacific herring were among the predominate fish species in stomachs of Pacific cod from Asian waters, and the crab *Chionoecetes* sp. was the most common invertebrate (Moiseev 1953). Flatfish and the sand lance, *Ammodytes* sp., however, appeared frequently in Moiseev's samples of Pacific cod stomachs but were rare or absent in my samples. The results of Jewett's (1978) study are in close agreement with the results of my study: he found fish, crab, and shrimp to be the most frequent items in Pacific cod stomachs collected near Kodiak, Alaska, during summer. In Jewett's study, walleye pollock was the most common fish eaten, and snow crab was the most common crab; Pacific herring were rarely eaten.

Other studies have demonstrated, as did my study, that larger codfishes become more piscivorous. As the size of Atlantic cod, *Gadus morhua*, increased, the diet changed from smaller invertebrates to larger fish (Powles 1958; Popova 1962; Rae 1967). Both Moiseev (1953) and Jewett (1978) found similar trends in their investigations of Pacific cod: cod <50-60 cm long ate mostly crustaceans; cod >60 cm primarily ate fish.

Some of the differences I found in foods of Pacific cod in outside and inside waters may be related to the availability of pandalid shrimp and Pacific herring. The results of my food study appear to reflect an increased abundance of both of these two foods in inside waters. Data from exploratory

TABLE 4.—Mean estimated percentage volume of food in stomachs of Pacific cod, by total length of cod and gear type, southeastern Alaskan waters, July 1977 (stomachs one-fourth full or greater).

	Outside waters						Inside waters					
	≤60 cm		61-70 cm		>70 cm		≤60 cm		61-70 cm		>70 cm	
Item	Nets	Traps	Nets	Traps	Nets	Traps	Nets	Traps	Nets	Traps	Nets	Traps
Fish	80.0	10.4	31.0	26.2	69.8	37.4	68.3	19.3	67.2	33.5	74.2	63.3
Crab	0	58.8	54.2	57.8	12.4	48.3	1.7	17.5	5.2	14.5	7.9	11.8
Shrimp	10.0	6.4	8.2	3.6	2.4	3.7	30.0	42.4	17.7	33.9	11.1	15.7
Pandalid	0	1.7	.6	.5	.4	2.4	30.0	8.4	16.2	24.2	8.0	14.5
Crangonid	10.0	3.6	3.0	2.6	1.6	1.3	0	17.5	1.5	2.9	1.5	.2
Hippolytid	0	1.1	.2	0	0	0	0	9.9	0	5.1	1.3	.6
Unidentified	0	0	4.4	.5	.4	0	0	6.6	0	1.7	.3	.4
Gammarid amphipods	5.0	8.8	.6	2.8	0	9.7	0	5.2	0	6.4	0	1.5
Mollusks												
Cephalopods	0	2.9	1.0	.3	.2	.3	0	3.0	9.6	4.5	4.6	3.5
Other mollusks	0	.8	0	1.7	.7	.3	0	6.0	.3	2.3	1.3	.9
Polychaetes	0	5.1	3.4	3.8	5.5	3	0	0	0	2.0	.1	0
Other foods and unidentified	5.0	6.8	1.6	3.8	9.0	0	0	6.6	0	2.9	.8	3.3
Cod caught (no.)	1	46	25	53	47	15	3	40	24	91	47	47
Mean total length (cm)	44.0	52.4	65.4	65.4	78.8	73.7	58.3	55.2	66.9	65.5	76.4	76.7

trawling surveys indicate pandalid shrimp are very low in abundance in outside waters (Schaefers and Smith 1954; Hitz and Rathjen 1965; Ronholt et al.[4]). From 1969 to 1975, no pandalid shrimp were commercially landed in this area (Ronholt et al. footnote 1). However, in the inside waters of southeastern Alaska around Petersburg, near the southern portion of my sample area, pandalid shrimp have been fished commercially since 1916 (Barr 1970). In northern inside waters, pandalid shrimp have also been reported as abundant (Ellson and Livingstone 1952). Similarly, since commercial fishing records were first kept in the 1920's, Pacific herring have been abundant in inside waters south of Cape Spencer (Reid 1971). No catches of Pacific herring have ever been reported for outside waters north of Cape Spencer apparently because of the scarcity of Pacific herring in this area.

Acknowledgments

I thank Don Mortensen of the Northwest and Alaska Fisheries Center Auke Bay Laboratory, NMFS, and the crew of the NOAA Ship *John N. Cobb* who collected the samples for this study, H. Richard Carlson who provided guidance throughout the study, Bruce Wing who aided in invertebrate indentification, and Lin Sonnenberg and Evan Haynes who reviewed the manuscript.

[4]Ronholt, L. L., H. H. Shippen, and E. S. Brown. 1976. An assessment of the demersal fish and invertebrate resources of the northeastern Gulf of Alaska. Yakutat Bay to Cape Cleare, May-August 1975. NEGOA Annual Report, 183 p. Processed rep. Northwest Fisheries Center, Natl. Mar. Fish. Serv., NOAA, 2725 Montlake Boulevard E., Seattle, WA 98112.

Literature Cited

ALVERSON, D. L., A. T. PRUTER, AND L. L. RONHOLT.
1964. A study of demersal fishes and fisheries of the northeastern Pacific Ocean. H.R. MacMillan Lect. Fish., Inst. Fish., Univ. B.C., Vancouver, 190 p.

BARR, L.
1970. Alaska's fishery resources. The shrimps. U.S. Fish Wildl. Serv., Fish. Leafl. 631, 10 p.

ELLSON, J. G., AND R. LIVINGSTONE, JR.
1952. The *John N. Cobb's* shellfish explorations in certain southeastern Alaskan waters, spring 1951. Commer. Fish. Rev. 14(4):1-20.

HITZ, C. R., AND W. F. RATHJEN.
1965. Bottom trawling surveys of the northeastern Gulf of Alaska (summer and fall of 1961 and spring of 1962). Commer. Fish. Rev. 27(9):1-15.

JEWETT, S. C.
1978. Summer food of the Pacific cod, *Gadus macrocephalus*, near Kodiak Island, Alaska. Fish. Bull., U.S. 76:700-706.

MOISEEV, P. A.
1953. Cod and flounders of far-eastern waters. Izv. Tikhookean. Nauchno-issled. Inst. Rybn. Khoz. Okeanogr. 40:1-287. (Translated from Russ., 1956, Fish. Res. Board Can. Transl. Ser. 119, Pt. I, 241 p.)

POPOVA, O. A.
1962. Some data on the feeding of cod in the Newfoundland area of the Northwest Atlantic. *In* Yu. Yu. Marti (editor), Soviet fishery investigations in the northwest Atlantic, p. 228-248. (Translated from Russ. by Isr. Program Sci. Transl., 1963, 370 p.; available U.S. Dep. Commer., Natl. Tech. Inf. Serv., Springfield, Va., as OTS 63-11102.)

POWLES, P. M.
1958. Studies of reproduction and feeding of Atlantic cod (*Gadus callarias* L.) in the southwestern Gulf of St. Lawrence. J. Fish. Res. Board Can. 15:1383-1402.

RAE, B. B.
1967. The food of cod in the North Sea and on the west of Scotland grounds. Dep. Agric. Fish. Scotl. Mar. Res. 1967(1), 68 p.

REID, G. M.
1971. Age composition, weight, length, and sex of herring,

Clupea pallasi, used for reduction in Alaska, 1929-66. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-634, 25 p.

SCHAEFERS, E. A., AND K. A. SMITH.

1954. Shellfish explorations in the Yakutat Bay area, Alaska, by the *John N. Cobb*, spring 1953. Commer. Fish. Rev. 16(3):1-12.

DAVID M. CLAUSEN

Northwest and Alaska Fisheries Center Auke Bay Laboratory
National Marine Fisheries Service, NOAA
P.O. Box 155
Auke Bay, AK 99821

USE OF GRIFFIN'S YIELD MODEL FOR THE GULF OF MEXICO SHRIMP FISHERY[1]

For analyzing the harvest of the Gulf of Mexico shrimp fishery, Griffin et al. (1976) have developed an equation that relates shrimp yield to freshwater discharge of the Mississippi River and fishing effort of Gulf shrimp vessels. The yield equation (referred to as Griffin's equation) is a modified Spillman production function (Heady and Dillon 1972). The Spillman function had its origin in agriculture where it was derived to predict the results of fertilizer experiments on tobacco yield in North Carolina. An important feature of the function is that it allows for environmental considerations in predicting yield. The modified form of the equation proposed by Griffin et al. (1976) is:

$$Y = \beta_0 D^{\beta_2} (1 - \beta_1^E) \quad (1)$$

where Y = yield of shrimp (million pounds),[2]
D = average daily discharge of the Mississippi River during the months that shrimp are in their nursery grounds (cubic feet per second),
E = vessel effort (thousand units),
$\beta_0, \beta_1, \beta_2$ = parameters to be estimated from data of the fishery.

The coefficients of Equation (1) were estimated from individual vessel records collected by the National Marine Fisheries Service and from measurements of water flow rates on the Mississippi River for the years 1962-74. According to Griffin and Beattie (1978), the fit was quite good, namely: "All estimated coefficients were significant at the 1% level; R^2 was 78.5; and the Durbin-Watson statistic was 2.25. The simple correlation coefficient between catch and effort was 0.64 and between catch and discharge was −0.63."

Griffin's equation has found numerous uses in the Gulf shrimp management literature. Griffin and Beattie (1978) used the equation to estimate the impact of effort reallocation as a result of Mexican extended jurisdiction; the Gulf Coast Research Laboratory at Ocean Springs, Miss., (Christmas and Etzold 1977) used the equation for similar purposes; and the Center for Wetland Resources, Louisiana State University[3] used the equation to estimate maximum sustainable yield for management considerations.

Despite the extensive usage, users have not critically reviewed Griffin's equation. Such a review is necessary because of the large-scale potential impact of proposed shrimp management plans. In view of this need, therefore, I subjected Griffin's equation to such a review.

The review consisted of two tests relevant to the usage of Griffin's equation in management decisions. In the first test, I estimated the error in expected yield introduced by the typical user who ignored the fact that the independent variables—effort and river discharge—have variances. For convenience, this was termed the "expected value test." In the second test, I depicted the error in yield estimate that would result from misspecification of model parameter estimates. For convenience, this test was termed the "sensitivity test."

The results were mixed. The expected value test produced a large absolute error in expected yield of shrimp. However, when compared with expected yield, the error was proportionally small. The sensitivity test produced some startling results. Yield turned out to be very significantly sensitive to a fixed model parameter whose constancy was conceptually questionable in the first place. This extreme sensitivity of yield raises questions regarding the reliability of Griffin's equation as a shrimp management tool.

Each test is discussed below in detail.

[1]Contribution No. 80-54M, Southeast Fisheries Center, National Marine Fisheries Service, NOAA, Miami, Fla.

[2]The original equation was estimated by Griffin et al. (1976) in nonmetric units and its nonlinear nature excludes conversion to metric units.

[3]Louisiana State University. 1979. Draft fishery management plan for shrimp fishery. Prepared by Center for Wetland Resources, L.S.U., Baton Rouge, 226 p.

Expected Value of Yield

Most users of Griffin's equation (Griffin et al. 1976; Louisiana State University (footnote 3) estimated yield by using the mean (or expected) value of the independent variables, discharge and effort. Yet it can easily be shown that, for a general two-variable function, if x, y are random variables and g an arbitrary twice differentiable function of x, y such that:

$$z = g(x,y) \tag{2}$$

then $$E[z] = E[g(x,y)] \neq g(E[x], E[y]) \tag{3}$$

or if $E[x] = \eta_x$ and $E[y]\ \eta_y$

then $$E[z] \neq g(\eta_x, \eta_y) \tag{4}$$

where $E(\cdot)$ denotes expectation of random variable.

Hence, yield estimates obtained using mean values as in Equation (4) are generally not accurate. It may be shown (Papoulis 1965) that Equation (4) may be correctly approximated as:

$$E[z] = g(\eta_x,\eta_y) + \frac{1}{2}\left\{\frac{\partial^2 g}{\partial x^2}\ \sigma_x^2 + \frac{\partial^2 g}{\partial y^2}\ \sigma_y^2 + \frac{2\partial^2 g}{\partial x \partial y}\ \mathrm{cov}\,(x,y)\right\} + \ldots \tag{5}$$

where the o^2's are the variances of variables x,y. The variance of the estimate is as follows:

$$\sigma_z^2 = \left\{\frac{\partial g}{\partial x}\right\}^2 \sigma_x^2 + \left\{\frac{\partial g}{\partial y}\right\}^2 \sigma_y^2 + 2\left\{\frac{\partial g}{\partial x}\ \frac{\partial g}{\partial y}\right\}\ \mathrm{cov}(x,y) + \ldots . \tag{6}$$

Thus, Equation (4) is only a first approximation, with Equation (5) providing the second term. Additional terms may be obtained by continuing Taylor's series expansion of $g(x,y)$ around $g(\eta_x, \eta_y)$. For the purpose of the test, however, the second term was sufficient.

For Griffin's equation the independent (random) variables were river discharge D and vessel effort E. So, the expected value of the dependent (random) variable yield Y could be expressed as:

$$E[Y] = Y(\eta_D,\eta_E) + \frac{1}{2}\left\{\frac{\partial^2 Y}{\partial D^2}\bigg|_{\eta_D}\ \sigma_D^2 + \frac{\partial^2 Y}{\partial E^2}\bigg|_{\eta_E}\ \sigma_D^2 + 2\frac{\partial^2 Y}{\partial D \partial E}\bigg|_{\eta_D,\eta_E}\ \mathrm{cov}\,(D,E)\right\}. \tag{7}$$

Similarly, the variance of the estimate was given by:

$$\sigma_y^2 = \left\{\frac{\partial Y}{\partial D}\right\}^2\bigg|_{\eta_D}\ \sigma_D^2 + \left\{\frac{\partial Y}{\partial E}\right\}^2\bigg|_{\eta_E}\ \sigma_E^2 + 2\left\{\frac{\partial Y}{\partial D}\cdot\frac{\partial Y}{\partial E}\right\}\bigg|_{\eta_D,\eta_E}\ \mathrm{cov}(D,E)\ . \tag{8}$$

To compute the estimated yield and its variance we required the first, second, and cross partial derivatives of the yield equation. The derivation was tedious and hence not reproduced here. By the necessary partial differentiation of Equation (1) we could write:

$$\frac{\partial Y}{\partial D} = \beta_2\beta_0 D^{\beta_2 - 1}\ (1 - \beta_1^E) \tag{9}$$

$$\frac{\partial^2 Y}{\partial D^2} = \beta_2\ (\beta_2 - 1)\ \beta_0 D^{\beta_2 - 2}\ (1 - \beta_1^E) \tag{10}$$

$$\frac{\partial Y}{\partial E} = -\beta_0 D^{\beta_2}\ \beta_1^E\ \log_e\beta_1 \tag{11}$$

$$\frac{\partial^2 Y}{\partial E^2} = -\beta_0 D^{\beta_2}\ \beta_1^E\ (\log_e\beta_1)^2 \tag{12}$$

$$\frac{\partial^2 Y}{\partial D \partial E} = -\beta_0\beta_2\ D^{\beta_2 - 1}\ \beta_1^E\ \log_e\beta_1\ . \tag{13}$$

Griffin et al. (1976) have estimated the equation parameters to be: $\beta_0 = 6593$, $\beta_1 = 0.995701$, and $\beta_2 = -0.60134$.

Expected yield of shrimp can be determined by using the means, variances, and covariances of river discharge and effort. Following the approach of one user of Griffin's equation (Christmas and Etzold 1977), yield was estimated by using mean values of variables for the years 1970-74. A listing of the data and numerical values of means and covariances are given in Table 1.

TABLE 1.—Data, including mean and variance of Mississippi River discharge (thousand cubic feet per second) at Tarbert Landing, Miss., and Gulf of Mexico commercial shrimp effort (thousands of days) from U.S. waters by vessel, 1970-74.[1]

	Discharge						
Year	Jan.	Feb	Mar	Apr	May	Mean Jan.-May	Effort
1970	448	430	529	652	852	582.2	249.1
1971	482	481	865	449	431	541.6	259.0
1972	560	427	602	536	749	574.8	282.6
1973	842	857	779	1,284	1,373	1,027	269.7
1974	971	1,083	828	792	576	850.00	243.6
Averages				ηD =	715.1	ηE =	260.8
SD				σD =	213.9	σE =	15.74
Covariance				$\mu D, E$ =	−141.92		

[1]Sources: U.S. Army Corps of Engineers, Stages and discharges of the Mississippi River and its tributaries and other watersheds in New Orleans District. U.S. Army Engineer District, New Orleans Corps of Engineers, Louisiana, and Christmas and Etzold 1977:28).

Appropriate insertion of these numerical values in Equation (7) produced the following estimates of yield:

$$E(Y) = 89.09 \text{ million lb}, \sigma_y^2 = 247.72.$$

Ignoring the variances and covariances, as most users of Griffin's equation do, we computed the corresponding estimated yield to be: $E(Y) = 85.48$ million lb.

The expected value test indicated that an absolute error of 3.6 million lb of shrimp is introduced by ignoring the variances and covariances of the independent variables. While an error of 3.6 million lb is large in absolute terms, its significance is diminished to 4% in relative terms. Furthermore, although 4% error is sizable, it is probably insufficient to alter economic management conclusions. We may conclude, therefore, that the expected value test, if applied to other applications of Griffin's equation, would not drastically alter management conclusions.

Parameter Sensitivity Test

Griffin's equation contains three parameters, each with its own significance and sensitivity. (Absolute and relative definitions of sensitivity can be found in Tomovic and Vukobratovic (1972) and Truxal (1972).) In assessing the sensitivity of yield to these parameters, I will relate proportional changes in parameter values to proportional changes in yield. (For this application of the sensitivity test, the relative measure of sensitivity is preferred because the results obtained are independent of the units of measure used for effort and discharge.) Mathematically, the sensitivity S of yield to parameter β may be expressed as:

$$S(Y|\beta) \triangleq \frac{\partial(\log_e Y)}{\partial(\log_e \beta)} = \frac{\partial Y/Y}{\partial\beta/\beta} = \frac{\partial Y}{\partial\beta} \cdot \frac{\beta}{Y}. \quad (14)$$

In considering parameter β_0, note that it is the dimensioned constant relating effort, discharge, and yield. The sensitivity of yield to β_0 is expressed:

$$S(Y|\beta_0) = 1.0. \quad (15)$$

In Equation (15), the sensitivity is small and constant. Thus, small errors in misspecification of β_0 will not significantly affect yield estimates.

Parameter β_2 governs the relationship between discharge of the Mississippi River and yield. Its sensitivity can be expressed as:

$$S(Y|\beta_2) = \beta_2 \log_e D. \quad (16)$$

The relationship is clearly linear and the sensitivity relatively small (Figure 1). Again, the implication being that misspecification of β_2 or future changes in its value would have small impact on yield.

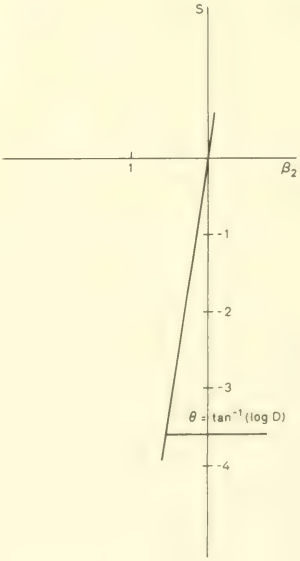


FIGURE 1.—Sensitivity (S) of yield to parameter β_2; i.e., the percentage change in yield corresponding to a 1% change in β_2.

The parameter β_1 is a little more difficult to understand. In the context of the model, β_1 is the constant that relates marginal yield corresponding to two successive units of effort. By appropriate manipulation of Equation (1) we can derive the following expression:

$$\beta_1 = \frac{\left.\frac{\partial Y}{\partial E}\right|_{\tilde{E}+1}}{\left.\frac{\partial Y}{\partial E}\right|_{\tilde{E}}}. \qquad (17)$$

Rational physical arguments may be used to show that β_1 is bounded by 0 and 1 ($0<\beta_1<1$). The law of diminishing returns provides the simplest argument, although there are others. Nevertheless, whatever the interpretation of β_1, sensitivity of yield to the parameter can be expressed as:

$$S(Y|\beta_1) = \frac{-E}{\beta_1^{-E}-1}. \qquad (18)$$

Since we have already established $0<\beta_1<1$, Equation (18) can be sketched as shown in Figure 2.

Yield is not very sensitive to β_1 for small values of $\beta_1 (\approx 0)$. The sensitivity increases hyperbolically, however, asymptotically approaching infinity as β_1 approaches the value unity.

Griffin's estimate of β_1 is 0.995701. This is about as close as one could get to the most sensitive region in Figure 2. For a value of effort E of 260.8, the sensitivity is −125.63. Thus any small misspecification of β_1 would produce very large errors in yield estimates.

It has already been shown that the parameter β_1 is related to marginal product of effort. At this point I question the assumption of β_1 as being a constant parameter. The marginal product of effort in any fishery is intimately related to stock and fleet characteristics. Realistically, one would expect marginal product and therefore its ratio to vary over time. Even if one could consider β_1 to be a constant over 1 yr, it would most certainly change over the course of the 12 yr that were used to estimate the given value (Griffin et al. 1976). Since I have already shown β_1 to be the most sensitive parameter of Griffin's equation, any misspecification or future change of β_1 would have enormous consequences on yield estimates.

Thus a user of Griffin's equation, who assumes a value of β_1 based on previous estimates of stock, effort, etc., may make incorrect predictions in the face of changing conditions. This observation severely limits the applicability of Griffin's equation for management purposes.

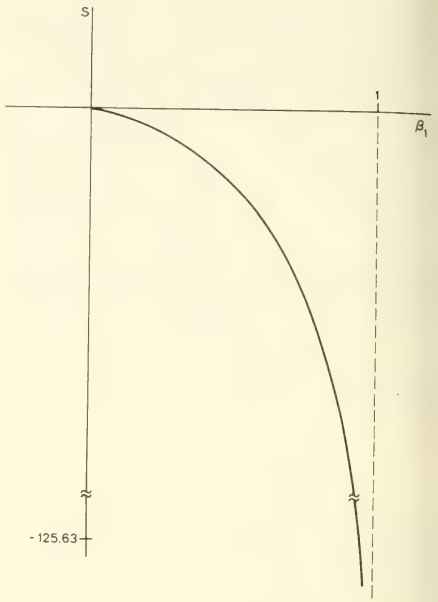


FIGURE 2.—Sensitivity (S) of yield to parameter β_1; i.e., the percentage change in yield corresponding to a 1% change in β_1.

Acknowledgments

I wish to express my thanks to Lynn M. Pulos who carefully critiqued several drafts of this paper. Her patience is much appreciated.

Literature Cited

CHRISTMAS, J. Y., AND D. J. ETZOLD (editors).
1977. The shrimp fishery of the Gulf of Mexico United States: A regional management plan. Gulf Coast Res. Lab., Tech. Rep. Ser. 2, 128 p.

GRIFFIN, W. L., AND B. R. BEATTIE.
1978. Economic impact of Mexico's 200-mile offshore fishing zone on the United States Gulf of Mexico shrimp fishery. Land Econ. 54:27-38.

GRIFFIN, W. L., R. D. LACEWELL, AND J. P. NICHOLS.
1976. Optimum effort and rent distribution in the Gulf of Mexico shrimp fishery. Am. J. Agric. Econ. 58:644-652.

HEADY, E. O., AND J. L. DILLON.
1972. Agricultural production functions. Iowa State Univ. Press, Ames, 667 p.
PAPOULIS, A.
1965. Probability, random variables and stochastic processes. McGraw-Hill, N.Y., 583 p.
TOMOVIC, R., AND M. VUKOBRATOVIC.
1972. General sensitivity theory. Am. Elsevier, N.Y., 258 p.
TRUXAL, J. G.
1972. Introductory systems engineering. McGraw Hill, N.Y., 596 p.

ARVIND KHILNANI

Southeast Fisheries Center Miami Laboratory
National Marine Fisheries Service, NOAA
75 Virginia Beach Drive, Miami, Fla.
Present address: *Department of Engineering-Economic Systems*
Stanford University, Stanford, CA 94305

SEASONAL SPAWNING CYCLE OF THE PACIFIC BUTTERFISH, *PEPRILUS SIMILLIMUS* (STROMATEIDAE)

There is little information on the reproductive biology of the Pacific butterfish, *Peprilus simillimus*, which ranges from Magdalena Bay, Baja California, to the Fraser River, British Columbia, and occurs at depths of 9-91 m (Miller and Lea 1972). It is commercially fished with purse seine, lampera, and bait net (Fitch and Lavenberg 1971). In 1976, 34.18 t were taken in California (Oliphant 1979). Fitch and Lavenberg (1971) reported spawning occurs in spring and extends perhaps into July. Horn (1970) studied the systematics and biology of the genus *Peprilus*. My purpose is to describe histologically the seasonal spawning cycle of the Pacific butterfish.

Methods

Fish were collected with the use of a lampera net between depths of 2 and 20 m from the vicinity of Oceanside, southern California (lat. 33°10′ N, long. 117°25′ W), during the period September 1978 through August 1979. Only female specimens were examined. Fish were fixed and preserved in 10% Formalin.[1] Ovarian histological sections from 232 specimens were cut at 8 μm and stained with iron hematoxylin. Seasonal gonosomatic indices (ovary weight/fish weight × 100) were calculated from preserved fish. Ovaries were histologically classified into four stages (Table 1).

TABLE 1.—Monthly distribution (percent) of ovarian stages in the yearly spawning cycle of *Peprilus simillimus*, September 1978-August 1979.

Month	*N*	Regressed or regressing	Pre-vitellogenic	Vitellogenic	Pre-spawning
Sept	25	100	0	0	0
Oct	18	100	0	0	0
Nov	15	100	0	0	0
Dec.	17	53	47	0	0
Jan	21	52	43	5	0
Feb.	19	26	42	16	16
Mar	20	10	15	0	75
Apr.	20	5	5	0	90
May	16	44	19	0	37
June	20	95	0	0	5
July	17	100	0	0	0
Aug	24	92	8	0	0

Results

Ovaries were regressed (Stage 1) during autumn (September-November) and consisted of primary oocytes <100 μm in diameter (Table 1). Gonosomatic indices (Figure 1) were reduced at this time. The first signs of ovarian activity for the new spawning cycle were noted during December. This was determined by an abundance of previtellogenic (vacuolated) (Stage 2) oocytes (130-200 μm) which typically appear before yolk deposition begins (Table 1). Enlarging (Stage 3) vitellogenic oocytes (yolk deposition in progress) were first noted in January. The first ripe (prespawning or gravid) (Stage 4) females with ovaries containing

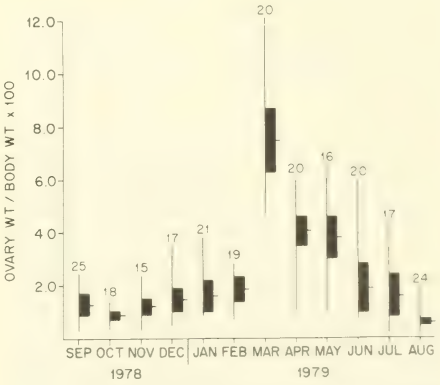


FIGURE 1.—Seasonal gonosomatic indices for *Peprilus simillimus*. Vertical line = range; horizontal line = mean; rectangle = 95% confidence interval. Sample size above each month.

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

mature yolk-filled oocytes (>400 μm) were collected in February. Since only a small fraction of my February sample was gravid, the spawning period for the majority of the population under study appeared to encompass March-May (Table 1). The smallest reproductively active female measured 114 mm standard length (SL); the largest 172 mm SL. Gonosomatic indices were at maximum sizes in March (Figure 1) and a progressive decrease was indicated through spring with minimal sizes occurring by June. A May increase in the incidences of follicular atresia indicated the end of spawning was near. Atretic oocytes are most abundant near the termination of spawning when oocytes that initiated but failed to complete yolk deposition degenerate.

My observation of follicles in various stages of yolk deposition during the spawning period suggests that successive batches of eggs are matured and spawned. The number of spawnings per individual per season are not known, but the presence of a mode of mature oocytes (imminent spawning), postovulatory follicles (transitory remnant of the follicle wall from a recent spawning), and a vitellogenic oocyte mode for a subsequent spawning indicates that females are capable of spawning more than once per season. Postovulatory follicles were similar in morphology to those reported in other teleosts (Hunter and Goldberg 1980).

Discussion

Peprilus simillimus undergoes a distinctly seasonal spawning cycle characterized by an abrupt increase in ovarian sizes during late winter with spawning essentially completed by the end of spring. Fitch and Lavenberg (1971) reported that spawning may extend into July. Horn (1970) similarly reported that spawning in *P. triacanthus*, *P. burti*, *P. paru*, and *P. simillimus* generally occurs in spring and early summer. This contracted type of cycle differs from that of some southern California fishes that have a considerably longer spawning period. Goldberg (1980) reported that gravid female *Chitonotus pugetensis* and *Icelinus quadriceriatus* (both Cottidae) were found throughout the year with maximum numbers in winter and early spring. The northern anchovy, *Engraulis mordax*, may have the ability to spawn all year but is likely limited by food availability and energy reserves (Brewer 1978; Hunter and Goldberg 1980).

The *P. simillimus* spawning cycle is more reminiscent of northern fishes (Quasim 1956), which have a short reproductive period (generally winter-early spring) with a single spawning. The multiple spawnings over a brief period exhibited by *P. simillimus* may represent a compromise between a short reproductive period with a single spawning (characteristic of high latitude fishes) and a long reproductive period with repeated spawnings typical of tropical fishes (Nikolsky 1963).

Acknowledgments

I am grateful to Edward DeMartini and Robert Fountain (University of California at Santa Barbara) for assistance in obtaining specimens. Trang Nguyen assisted with histological preparations. This study was aided by a Whittier College faculty research grant.

Literature Cited

BREWER, G. D.
1978. Reproduction and spawning of the northern anchovy, *Engraulis mordax*, in San Pedro Bay, California. Calif. Fish Game 64:175-184.

FITCH, J. E., AND R. J. LAVENBERG.
1971. Marine food and game fishes of California. Univ. Calif. Press, Berkeley, 179 p.

GOLDBERG, S. R.
1980. Seasonal spawning cycles of two marine cottid fishes, *Chitonotus pugetensis* and *Icelinus quadriceriatus* from southern California. Bull. Mar. Sci. 30:131-135.

HORN, M. H.
1970. Systematics and biology of the stromateid fishes of the genus *Peprilus*. Bull. Mus. Comp. Zool. 140:165-261.

HUNTER, J. R., AND S. R. GOLDBERG.
1980. Spawning incidence and batch fecundity in northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 77:641-652.

MILLER, D. J., AND R. N. LEA.
1972. Guide to the coastal marine fishes of California. Calif. Dep. Fish Game, Fish Bull. 157, 235 p.

NIKOLSKY, G. V.
1963. The ecology of fishes. Acad. Press, N.Y., 352 p.

OLIPHANT, M. S.
1979. California marine fish landings for 1976. Calif. Dep. Fish Game, Fish Bull. 170, 56 p.

QUASIM, S. Z.
1956. Time and duration of the spawning season in some marine teleosts in relation to their distribution. J. Cons. 21:144-154.

STEPHEN R. GOLDBERG

Department of Biology
Whittier College
Whittier, CA 90608

EFFECTS OF INJURIES ON SPINY LOBSTER, *PANULIRUS ARGUS*, AND IMPLICATIONS FOR FISHERY MANAGEMENT

The spiny lobster, *Panulirus argus*, supports important commercial and recreational fisheries throughout its range from Bermuda to Brazil. Its ecology and physiology are typical of a number of other commercially important palinurid species, which collectively have pantropic distributions (Phillips and Cobb 1977).

A variety of decapod crustacean responses to injuries, primarily limb loss, have been recorded. Aiken (1977) summarized a number of studies conducted in laboratories, some of which found that limb loss greatly accelerated ecdysis. Other observers noted limb loss resulted in reduced growth rates (Chittleborough 1975; Ford 1977; Savage and Sullivan 1978). This paper reports the effects of injuries on growth rates of wild juvenile spiny lobsters, *P. argus*, in Florida and discusses the implications of these effects on *P. argus* biology and its fishery.

Spiny lobsters (Palinuridae) have complex life cycles. Larval, early juvenile, and adult stages of the spiny lobster in Florida, *P. argus*, are ecologically dissimilar and are found separately in relatively discrete habitats. The planktonic phyllosoma larvae spend 5 to 9 mo in the open ocean before metamorphosing into actively swimming postlarvae, called pueruli (Lewis 1951). Pueruli swim into shallow coastal waters where they settle onto the bottom, assuming the benthic existence they will follow the rest of their lives. Postlarval and small juvenile spiny lobsters are found scattered throughout seagrass beds, particularly in shallow inshore areas like Biscayne Bay. Larger juveniles concentrate around rocky outcrops, sponges, and groups of sea urchins for shelter during the day (Khandker 1964; Davis 1971; Berrill 1975). They forage nightly on adjacent grassbeds and open sand areas for small mollusks, echinoids, and crustaceans (Herrnkind et al. 1975). Mature lobsters are generally associated with coral reefs, or other hard bottom, offshore to depths >150 m. The transition from inshore juvenile habitat to habitat offshore is sometimes accomplished by spectacular mass migrations, marked by long queues of lobsters (Herrnkind and Cummings 1964; Kanciruk and Herrnkind 1978).

The fishing season for *P. argus* in Florida extends slightly more than 8 mo from late July through March, with a special 2-d sport fishing season 5 d prior to the beginning of the regular sport and commercial season (Florida Statute 370.14). Recreational diving activity directed at spiny lobster harvest is particularly intense in nearshore areas during the first 6 to 8 wk of each season (Austin 1976). There are also over 1,000 commercial trappers, fishing up to 2,000 traps each, in the fishery (Beardsley et al. 1975).

Methods

At weekly or monthly intervals during 1976 and 1977, spiny lobsters were captured in southern Biscayne Bay, Fla., by hand, bully net, or tail snare and marked with spaghetti tags. The details and efficacy of this tagging procedure were reported by Davis (1978). Data on size (as carapace length, CL), injuries, molt condition, location, and water temperature were recorded. Injuries were recorded as the number of missing legs or antennae, or damage to the abdomen, cephalothorax, or supraorbital horns.

Growth of spiny lobsters takes place as the result of a series of molts, during which discontinuous size changes occur. The rate of growth is dependent on both magnitude of change in size with each molt (molt increment) and the length of the intermolt period. In this study, growth rate was expressed as change in carapace length per week, since nearly all observations of marked lobsters were made at weekly intervals. To reduce the variability inherent in measuring discontinuous changes in carapace length that resulted from random observations of growth during the molting cycle, all changes in size were summed over each class of observations (i.e., winter, summer, injured, or uninjured) and expressed as rates per week.

Results

A total of 7,643 *P. argus* were examined from February 1976 to December 1977. They ranged from 15 to 101 mm CL, with a mean of 60.7 mm CL (Table 1). Mean monthly water temperatures varied from 16° to 32° C.

Observations of growth were made for 844 time intervals, ranging from 1 to 82 wk (mean 20 wk), on 534 individual lobsters in the wild, ranging from 38 to 83 mm CL. Carapace length measurements were replicated by independent observers on the same day for 153 lobsters during the 22-mo tagging period to evaluate the precision of the carapace length measurements by various

TABLE 1.—Monthly summary of size, molting activity, and condition of spiny lobsters, and water temperatures in eastern Biscayne Bay, Fla., 1976-77.

Month	Number of lobsters	Size (mm CL)			Percentage		Mean water temp (°C)
		Min	Max	Mean	Molting	Injured	
1976:							
Feb.	1,247	34	84	56.1	8	53	16
Mar.	353	33	83	56.4	9	51	26
Apr.	464	38	86	60.0	12	45	25
May	362	34	79	59.4	12	39	27
June	340	43	87	63.2	14	46	29
July	414	15	85	61.6	8	31	31
Aug.	398	37	83	63.5	7	38	31
Sept.	217	40	96	63.1	6	42	30
Oct.	25	35	89	64.6	12	24	26
Dec.	139	38	85	54.7	13	42	17
1977:							
Jan.	86	33	85	57.7	43	37	16
Feb.	619	30	81	55.5	11	50	18
Mar.	387	31	88	57.3	7	49	23
Apr.	272	39	80	59.2	12	47	25
May	220	39	101	61.8	17	40	26
June	268	27	85	63.6	26	41	28
July	322	35	86	62.1	8	35	32
Aug.	414	30	84	63.6	17	31	32
Sept.	454	30	97	66.9	11	29	30
Oct.	335	32	99	65.3	13	35	27
Nov.	307	32	92	60.1	2	41	24
Total	7,643						
Mean		33.6	87.4	60.7	12.8	40.3	25.7

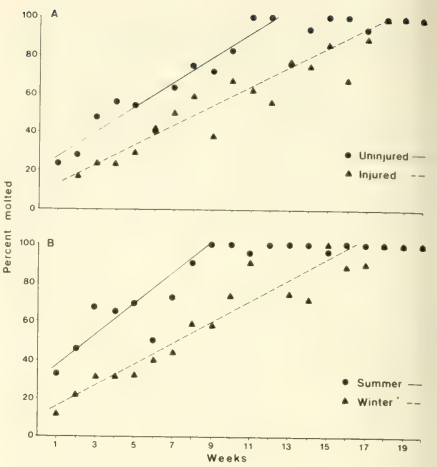


FIGURE 1.—Comparison of molting activity as a function of condition (A) and season (B) for spiny lobsters in Biscayne Bay, Fla.

technicians. The mean error was 0.3 mm, with a range of −1.8 to +2.1 mm. Consequently, only changes in carapace measurements >2.0 mm were recorded as growth, others were considered measurement errors.

Two factors appeared to affect growth rates: water temperature and lobster condition. Growth rate did not vary with either sex or size within the range observed. Mean intermolt periods were estimated by doubling the time interval over which 50% of the lobsters observed had molted. This assumed that at the time of tagging the lobsters were randomly distributed throughout their molting cycle (Munro 1974). This appeared reasonable since we observed molting activity throughout the year (Table 1), and direct observations of individual lobsters through periodic recaptures confirmed the mean values obtained for the population in this manner (Davis 1978). For example, during winter, the percentage of tagged lobsters that had molted increased weekly from 12% after 1 wk to 22, 31, 32, 40, 44, and 58% after 8 wk, indicating that 50% had molted after about 7.5 wk, resulting in a mean intermolt period of 15 wk (Figure 1). In contrast, the mean intermolt period during summer was only 8 wk (Table 2). The mean intermolt period of injured lobsters was 15 wk, and for uninjured lobsters it was 10 wk (Table 2). The mean growth increments were estimated by examining frequency distributions of observed changes in carapace length. Mean single molt growth increments were significantly larger during the summer and for uninjured lobsters than during the winter and for injured lobsters, respectively (Table 3). Effects of season and lobster condition on growth rate were independent (Table 4).

TABLE 2.—Mean growth variables determined from 1,688 observations on 534 tagged juvenile spiny lobsters in Biscayne Bay, Fla., 1976-1977.

Item	Number of growth intervals observed	Intermolt period (wk)	Observed growth rate (mm CL/wk)	Water temp (°C)
Season:				
Winter	656	15	0.31	21.1
Summer	146	8	0.75	29.1
Condition:				
Injured	465	15	0.31	[1]
Uninjured	379	10	0.51	[1]
All observations	844	12	0.41	25.7

[1]Not available.

Predictably, higher summer (May-October) temperatures and longer daylight periods were related to a greater growth rate (0.75 mm CL/wk) than that observed during winter, November through April (0.31 mm CL/wk). This 59% decrease in growth rate between summer and winter was apparently related to the 8.0° C decrease in mean water temperature, from 29.1° to 21.1° C, and the increased frequency of injuries incurred dur-

TABLE 3.—Comparison of mean molt increments (millimeters of change in carapace length) of juvenile spiny lobsters, in Biscayne Bay, Fla.

Item	Season		Conditions	
	Summer	Winter	Injured	Uninjured
$\bar{x}$	6.0	4.7	4.7	5.2
Sx	3.2	3.6	3.8	3.8
t, 306 df	7.75**		2.25*	

**$P \leq 0.01$; *$P \leq 0.05$.

TABLE 4.—Two-way fixed factor ANOVA of effects of season and spiny lobster condition as evidenced by growth rate.

Source of variation	df	SS	MS	F
Subgroups	3	106.50	35.50	
A (columns; condition)	1	34.60	34.60	4.65*
B (rows; season)	1	68.67	68.67	9.23**
A × B (interaction)	1	3.23	3.23	0.43n.s.
Within subgroups (error)	3,784	28,249.73	7.44	
Total	3,787	28,356.23		

*$P \leq 0.05$; **$P \leq 0.01$.

ing the fall and winter fishing season. Growth rates were lowest for injured lobsters during winter and highest for uninjured animals during summer, but injured lobsters grew faster in summer than injured ones in winter. Both of these factors, reduced temperature and injuries, caused increased intermolt periods and reduced molt increments, which resulted in reduced growth rates (Table 2). Change in the length of the intermolt period was the major effect of both factors, but by inspection of the values in Tables 2 and 3, it was apparent that intermolt period was proportionately more important for the injury-caused reduction, whereas decreased molt increment was proportionately more important for the season-related growth reduction.

Discussion

The growth data presented here generally conform both in magnitude and character to that in the published literature for decapod crustaceans, but the precise effect of injuries in the wild and definition of their origin is apparently new information, particularly for *P. argus*. Estimated growth rates for juvenile *P. argus* in the Caribbean, Florida, and Bermuda, range from 0.43 to 0.65 mm CL/wk (Smith 1951; Travis 1954; Sutcliffe 1957; Buesa M. 1965; Witham et al. 1968; Sweat 1968; Little 1972; Eldred et al. 1972; Ting 1973; Munro 1974; Peacock 1974; Olsen and Koblic 1975). The estimates for Biscayne Bay from this study ranged from 0.31 to 0.75 mm CL/wk, but the mean of 0.41 mm CL/wk was the lowest reported. The 1977 winter in Biscayne Bay was the coldest in the previous century (Molinari et al. 1977; McGuirk 1978), and the Bay is already near the northern limit of *P. argus* distribution. That cold winter depressed the mean growth rate somewhat, but another significant factor was that the Biscayne Bay lobster population was the most heavily fished by sport divers of all of those for which growth rates were reported. The injuries resulting from diver activity also depressed the growth rate. It appeared that a combination of cold weather and extremely high fishing activity caused the low growth rate reported in this study.

Variations in growth rates of lobsters have been attributed to several factors, the most common of which is temperature (Crawford and De Smidt 1922; Newman and Pollock 1974; Phillips et al. 1977). Limited food (Sutcliffe 1957; Chittleborough 1970; Newman and Pollock 1974), shelter (Chittleborough 1970), salinity and light (Travis 1954), and injuries (Chittleborough 1974a; Aiken 1977; Ford 1977) have also been cited as factors affecting lobster growth (see Aiken 1977, Dall 1977, and Ford 1977 for a review of lobster growth). The effects of these factors are translated into growth rate variations by changing either intermolt period, molt increment, or both. Most commonly, intermolt is shortened by warm temperatures, darkness, or autotomy of appendages; and lengthened by age, cold, or low salinity. Under some conditions, as in this study, both changes in molt increment and intermolt period occurred (Mauviot and Castell 1976; Aiken 1977; Pollock and Roscoe 1977).

While autotomy may stimulate molting, Chittleborough (1974a) reported that repeated loss of two or three legs or a large number of appendages resulted in decreased molt increment, so the net result was a reduction in growth rate. The results of the current study in Biscayne Bay also clearly demonstrated the adverse impact of injuries on growth rates. However, our observations did not demonstrate any proportional relationship between the degree of injury and the degree of molt increment depression as demonstrated for shore crabs by Kuris and Mager (1975). Most injured lobsters in Biscayne Bay were missing one or both antennae and one or two legs. The growth rate of *P. argus* with these minor injuries, five or fewer missing appendages, was virtually identical to the growth rate of more seriously injured lobsters that survived and which were missing up to nine legs and both antennae. It appeared that even minor losses caused a significant shift in growth pattern.

At the mean growth rate of 0.51 mm CL/wk observed for uninjured lobsters, it took about 51 wk for a juvenile to reach the minimum legal size of 76.2 mm CL from a size of 50 mm CL at age 2 (Lewis 1951; Sweat 1968). At 50 mm CL they began to associate gregariously with the larger juveniles in the eastern bay where they were subjected to fishery pressure. At the injury-depressed growth rate of 0.31 mm CL/wk, it required 84 wk to reach legal harvest size and enter the fishery 33 wk later than uninjured lobsters. During the additional 33 wk required to reach legal harvest size, natural mortality from groupers and other predators undoubtedly eliminated significant numbers of lobsters before they could enter the fishery. Olsen and Koblic (1975) estimated natural mortality of juvenile *P. argus* in Virgin Islands National Park at 34.8%/yr, at that rate, about 22% (33/52 of annual mortality) of the injured lobsters in Biscayne Bay were lost to the fishery as a direct result of their injuries. By the end of the open season, about half of the lobsters in Biscayne Bay were missing several legs and/or antennae. The frequency of injured lobsters dropped through the 4-mo closed season to about 30%, as the population molted at least once without harrassment from fishermen (Table 1). Less than 25% of 963 juvenile lobsters examined from an unfished population at Dry Tortugas, Fla., displayed similar injuries, which were presumably due to encounters with natural predators, difficulties with molting, or other normal stresses (Davis unpubl. data). Fishery induced injuries reduced the yield per postlarval recruit by reducing growth rate and consequently allowing natural mortality to occur over a significantly longer than normal period of time.

Another aspect of injury slowed growth rates is its effect on size of maturity. Maturity in spiny lobsters is apparently more a function of age than size (Chittleborough 1974b). Therefore if growth rate is significantly reduced by fishing activities through injuries, the size of mature lobsters would be reduced in areas of intense fishing activity. In the light to moderately fished Dry Tortugas fishery, the size of first maturity of female *P. argus* was about 90 mm CL for most of the population (78 mm CL smallest ovigerous) (Davis 1975). In the intensely fished lower keys fishery, the size of first maturity was reported at about 80 mm CL (smallest ovigerous 71.4 mm CL) (Warner et al. 1977). However, while age induces onset of maturity, female size is a major limit to fecundity. Creaser (1950) pointed out that a single 130 mm CL female *P. argus* produced as many eggs as four 87 mm CL females. Under the same environmental conditions, a population of injury-stunted lobsters could not produce the number of larvae that a population of normal-sized animals would (Kanciruk and Herrnkind 1976). Spawning fewer larvae may also result in reduced genetic diversity in the *P. argus* population, which would have further detrimental consequences for the management of this valuable resource (Miller 1979).

Intense fishing pressure on commercial concentrations of spiny lobsters inflicts injuries in several ways. Recreational divers inadvertently damage juvenile lobsters in attempting to catch associated larger animals, and by repeatedly catching nearly legal-sized lobsters to measure them. Florida law permits the capture, transportation, and use of sublegal-sized juveniles for attractors (bait) in commercial traps (Florida Statute 370.14), and juveniles are occasionally caught in traps along with adults. These sources of injury to the lobsters are all amenable to standard lobster trap fishery management techniques. Escape vents on traps that would allow small lobsters to leave and a prohibition on handling and transporting juvenile lobsters could eliminate the sources of injury from the trapping segment of the fishery (Bowen 1971). Nursery sanctuaries in which no fishing activity is allowed, and regulations prohibiting the use of hooks and spears by divers could eliminate diver and trap induced injuries.

The response of *P. argus* to injuries is probably representative of most tropical palinurids, and the information developed here could have wide application for fisheries management.

Acknowledgments

I would like to thank G. Y. Hendrix and J. A. Kushlan for their assistance and encouragement, and W. F. Herrnkind and P. Kanciruk for their helpful critical review of the manuscript.

Literature Cited

AIKEN, D. E.
1977. Molting and growth in decapod crustaceans, with particular reference to the lobster *Homarus americanus*. *In* B. F. Phillips and J. S. Cobb (editors), Workshop on lobster and rock lobster ecology and physiology, p. 41-74. CSIRO Div. Fish. Oceanogr. Circ. 7.

AUSTIN, C. B.
1976. Recreational boating in Biscayne Bay. *In* A. Thorhaug and A. Volker (editors), Biscayne Bay: Past/

Present/Future, p. 247-253. Univ. Miami Sea Grant Spec. Rep. 5.

BEARDSLEY, G. L., T. J. COSTELLO, G. E. DAVIS, A. C. JONES, AND D. C. SIMMONS.
1975. The Florida spiny lobster fishery. A white paper. Fla. Sci. 38:144-149.

BERRILL, M.
1975. Gregarious behavior of the spiny lobster, *Panulirus argus* (Crustacea: Decapoda). Bull. Mar. Sci. 25:515-522.

BOWEN, B. K.
1971. Management of the western rock lobster (*Panulirus longipes cygnus*, George). Proc. Indo-Pac. Fish. Counc. 14(II):139-153.

BUESA, R. J.
1965. Biology and fishing of spiny lobster *Panulirus argus* (Latreille). *In* A. S. Bogdanov (editor), Soviet-Cuban fishery research. (Translated from Russian by Isr. Program Sci. Transl., 1969, p. 62-77, as TT 69-59016.)

CHITTLEBOROUGH, R. G.
1970. Studies on recruitment in the Western Australian rock lobster *Panulirus longipes cygnus* George: density and natural mortality of juveniles. Aust. J. Mar. Freshwater Res. 21:131-148.
1974a. Review of prospects for rearing rock lobsters. Aust. Fish. 33(4):4-8.
1974b. Western rock lobster reared to maturity. Aust. J. Mar. Freshwater Res. 25:221-225.
1975. Environmental factors affecting growth and survival of juvenile western rock lobsters *Panulirus longipes* (Milne-Edwards). Aust. J. Mar. Freshwater Res. 26:177-196.

CRAWFORD, D. R., AND W. J. J. DE SMIDT.
1922. The spiny lobster, *Panulirus argus*, of southern Florida: its natural history and utilization. Bull. U.S. Bur. Fish. 38:281-310.

CREASER, E. P.
1950. Repetition of egg-laying and number of eggs of the Bermuda spiny lobster. Proc. Gulf Caribb. Fish. Inst. 2:30-31.

DALL, W.
1977. Review of the physiology of growth and moulting in rock lobsters. *In* B. F. Phillips and J. S. Cobb (editors), Workshop on lobster and rock lobster ecology and physiology, p. 75-82. CSIRO Div. Fish. Oceanogr. Circ. 7.

DAVIS, G. E.
1971. Aggregations of spiny sea urchins, *Diadema antillarum*, as shelter for young spiny lobsters, *Panulirus argus*. Trans. Am. Fish. Soc. 100:586-587.
1975. Minimum size of mature spiny lobsters, *Panulirus argus*, at Dry Tortugas, Florida. Trans. Am. Fish. Soc. 104:675-676.
1978. Field evaluation of a tag for juvenile spiny lobsters, *Panulirus argus*. Trans. Am. Fish. Soc. 107:100-103.

ELDRED, B., C. R. FUTCH, AND R. M. INGLE.
1972. Studies of juvenile spiny lobsters, *Panulirus argus*, in Biscayne Bay, Florida. Fla. Dep. Nat. Resour., Mar. Res. Lab., Spec. Sci. Rep. 35, 15 p.

FORD, R. E.
1977. Growth patterns of lobsters. *In* B. F. Phillips and J. S. Cobb (editors), Workshop on lobster and rock lobster ecology and physiology, p. 83-102. CSIRO Div. Fish. Oceanogr. Circ. 7.

HERRNKIND, W. F., AND W. C. CUMMINGS.
1964. Single file migrations of the spiny lobster, *Panulirus argus* (Latreille). Bull. Mar. Sci. Gulf Caribb. 14:123-125.

HERRNKIND, W. F., J. A. VANDERWALKER, AND L. BARR.
1975. Population dynamics, ecology and behavior of spiny lobsters, *Panulirus argus*, of St. John, U.S. V.I.: (IV) Habitation, patterns of movement and general behavior. *In* S. A. Earle and R. J. Lavenberg (editors), Results of the Tektite program: coral reef invertebrates and plants, p. 31-45. Nat. Hist. Mus. Los Ang. Cty., Sci. Bull. 20.

KANCIRUK, P., AND W. F. HERRNKIND.
1976. Autumnal reproduction in *Panulirus argus* at Bimini, Bahamas. Bull. Mar. Sci. 26:417-432.
1978. Mass migration of spiny lobster, *Panulirus argus* (Crustacea: Palinuridae): behavior and environmental correlates. Bull. Mar. Sci. 28:601-623.

KHANDKER, N. A.
1964. Sponge as a shelter for young spiny lobster. Trans. Am. Fish. Soc. 93:204.

KURIS, A. M., AND M. MAGER.
1975. Effect of limb regeneration on size increase at molt of the shore crabs *Hemigrapsus oregonensis* and *Pachygrapsus crassipes*. J. Exp. Zool. 193:353-359.

LEWIS, J. B.
1951. The phyllosoma larvae of the spiny lobster *Panulirus argus*. Bull. Mar. Sci. Gulf Caribb. 1:89-103.

LITTLE, E. J.
1972. Tagging of spiny lobsters (*Panulirus argus*) in the Florida Keys, 1967-1969. Fla. Dep. Nat. Resour., Spec. Sci. Rep. 31, 23 p.

MAUVIOT, J. C., AND J. D. CASTELL.
1976. Molt- and growth-enhancing effects of bilateral eyestalk ablation on juvenile and adult American lobsters (*Homarus americanus*). J. Fish. Res. Board Can. 33:1922-1929.

MCGUIRK, J. P.
1978. Planetary-scale forcing of the January 1977 weather. Science (Wash., D.C.) 199:293-295

MILLER, R. I.
1979. Conserving the genetic integrity of faunal populations and communities. Environ. Conserv. 6:297-304.

MOLINARI, R. L., S. BAIG, D. W. BEHRINGER, G. A. MAUL, AND R. LEGECKIS.
1977. Winter intrusions of the loop current. Science (Wash., D.C.) 198:505-507.

MUNRO, J. L.
1974. The biology, ecology, exploitation and management of Caribbean reef fishes. Scientific Rep. of the ODA/UWI Fisheries Ecology Research Proj., 1962-1973. Part V.1. The biology, ecology, and bionomics of Caribbean reef fishes crustaceans (spiny lobsters and crabs). Univ. West Indies Zool. Dep. Res. Rep. 3, 57 p.

NEWMAN, G. G., AND D. E. POLLOCK.
1974. Biological cycles, maturity and availability of rock lobster, *Jasus lalandii* on two South African fishing grounds. S. Afr. Sea Fish. Branch Invest. Rep. 107:1-16.

OLSEN, D. A., AND I. G. KOBLIC.
1975. Population dynamics, ecology and behavior of spiny lobsters, *Panulirus argus*, of St. John, U.S. V.I.: (II) Growth and mortality. *In* S. A. Earle and R. J. Lavenberg (editors), Results of the Tektite program: coral reef invertebrates and plants, p. 17-21. Nat. Hist. Mus. Los Ang. Cty., Sci. Bull. 20.

PEACOCK, N. A.
1974. A study of the spiny lobster fishery of Antigua and Barbuda. Proc. Gulf Caribb. Fish. Inst. 26:117-130.
PHILLIPS, B. F., N. A. CAMPBELL, AND W. A. REA.
1977. Laboratory growth of early juveniles of the western rock lobster *Panulirus longipes cygnus*. Mar. Biol. (Berl.) 39:31-39.
PHILLIPS, B. F., AND J. S. COBB (editors).
1977. Workshop on lobster and rock lobster ecology and physiology. CSIRO Div. Fish. Oceanogr. Circ. 7, 300 p.
POLLOCK, D. E., AND M. J. ROSCOE.
1977. The growth at molting of crawfish *Jasus tristani* at Tristan da Cunha, South Atlantic. J. Cons. 37:144-146.
SAVAGE, T., AND J. R. SULLIVAN.
1978. Growth and claw regeneration of the stone crab, *Menippe mercenaria*. Fla. Mar. Res. Publ. 32, 23 p.
SMITH, F. G. W.
1951. Caribbean spiny lobster investigations. Proc. Gulf Caribb. Fish. Inst., 3d Annu. Sess., p. 128-134.
SUTCLIFFE, W. H., JR.
1957. Observations on the growth rate of the immature Bermuda spiny lobster, *Panulirus argus*. Ecology 38:526-529.
SWEAT, D. E.
1968. Growth and tagging studies on *Panulirus argus* (Latreille) in the Florida Keys. Fla. Board Conserv., Tech. Ser. 57, 30 p.
TING, R. Y.
1973. Investigation on the resource potential of the spiny lobster (*Panulirus argus* Latreille) in Puerto Rico. Contrib. Agropec. Pesq. Organo Of. Serv. Aux. Oper. Cent. 5(2):1-18.
TRAVIS, D. F.
1954. The molting cycle of the spiny lobster, *Panulirus argus* Latreille. I. Molting and growth in laboratory-maintained individuals. Biol. Bull. (Woods Hole) 107:433-450.
WARNER, R. E., C. L. COMBS, AND D. R. GREGORY, JR.
1977. Biological studies of the spiny lobster, *Panulirus argus* (Decapoda; Palinuridae), in south Florida. Proc. 29th Annu. Sess. Gulf Caribb. Fish. Inst., p. 166-183.
WITHAM, R., R. M. INGLE, AND E. A. JOYCE, JR.
1968. Physiological and ecological studies of *Panulirus argus* from the St. Lucie estuary. Fla. Board Conserv. Mar. Lab. Tech. Ser. 53, 31 p.

GARY E. DAVIS

U.S. National Park Service, South Florida Research Center
Everglades National Park
Homestead, Fla.
Present address: *Channel Islands National Park*
1699 Anchors Way Drive
Ventura, CA 93003

INDEX

Fishery Bulletin Vol. 78, 1-4

ADAMS, PETER B., "Life history patterns in marine fishes and their consequences for fisheries management" 1

ADAMS, PETER B.—see LENARZ and ADAMS

"Additional records of the sculpin *Psychrolutes phrictus* in the eastern Bering Sea and off Oregon," by Ann C. Matarese and David L. Stein ... 169

AINLEY, DAVID G., CRAIG S. STRONG, HARRIET R. HUBER, T. JAMES LEWIS, and STEPHEN H. MORRELL, "Predation by sharks on pinnipeds at the Farallon Islands" ... 941

Alaska, southeastern
  cod, Pacific
    summer food ... 968

ALEVIZON, WILLIAM S.—see EBELING et al.

AMBLER, JULIE W., "Species of *Munidopsis* (Crustacea, Galatheidae) occurring off Oregon and in adjacent waters" ... 13

"Ammonia concentrations in pink salmon, *Oncorhynchus gorbuscha*, redds of Sashin Creek, southeastern Alaska," by Stanley D. Rice and Jack E. Bailey ... 809

"(An) analysis of the United States demand for fish meal," by D. D. Huppert ... 267

Anchovy, northern
  changes in body measurements of larvae due to handling and preservation
    eye diameter ... 690
    laboratory shrinkage ... 687
    live body parts ... 686
    net-treatment shrinkage ... 688
    preservation shrinkage (after net treatment) ... 690
  direct method for estimating spawning biomass ... 541
  effects of copper on early life history stages ... 675
  egg cannibalism ... 811
  larvae, percentage of starving in southern California Bight
    classification of larvae ... 481
    digestive tract ... 479
    geographical distribution ... 481
    other organs ... 481
    plankton volume ... 486
    standard length ... 481
    surface temperature ... 485
    trunk musculature ... 476
  reproduction off Oregon and Washington
    fecundity ... 611
    gonadal condition ... 606
    length and age at sexual maturity ... 606
    ovarian maturation ... 607
    seasonal distribution ... 615
    sex ratio ... 607
    spawning frequency ... 612
  respiration and depth control as possible reasons for swimming of larvae ... 109
  spawning biomass and early life off Oregon and Washington
    comparison of northern and central subpopulations 871
    egg and larva census estimates ... 858, 867
    field procedures ... 857
    hydrography and plankton volume ... 862
    laboratory procedures ... 858
    larval transport and juvenile nurseries ... 873
    relationship with Columbia River plume ... 872
    spawning biomass estimates ... 859, 868
    subpopulation, northern ... 856
    yield estimates ... 862, 870

Anglerfishes, ceratioid
  Philippine Archipelago
    Caulophrynidae ... 380
    Caulophrynidae genera and species key ... 380
    Centrophrynidae ... 395
    Ceratiidae ... 395
    Ceratiidae genera and species key ... 395
    Ceratioidei family key ... 379
    Diceratiidae ... 381
    Diceratiidae genera and species key ... 381
    Gigantactinidae ... 396
    Himantolophidae ... 381
    Linophrynidae ... 396
    Linophrynidae genera and species key ... 396
    Melanocetidae ... 381
    Melanocetus species key ... 381
    Oneirodes species key ... 382
    Oneirodidae ... 382
    Oneirodidae genera key ... 382
    Thaumatichthyidae ... 395
  systematics and distribution
    distribution ... 83
    evolutionary relationships ... 84
    genus *Melanocetus* ... 70
    key to species based on females ... 70
    Melanocetus eustalus n. sp. ... 79
    Melanocetus johnsoni ... 71
    Melanocetus murrayi ... 81
    Melanocetus niger ... 78
    Melanocetus polyactis ... 77
    Melanocetus species ... 83
    osteology of females ... 61
    type genus *Melanocetus* ... 67

"Annual variability of reef-fish assemblages in kelp forests off Santa Barbara, California," by Alfred W. Ebeling, Ralph J. Larson, William S. Alevizon, and Richard N. Bray 361

"Aspects of larval ecology of *Squilla empusa* (Crustacea, Stomatopoda) in Chesapeake Bay," by Steven G. Morgan 693

ASPER, EDWARD D.—see ODELL et al.

Atlantic Bight, Middle
Callinectes larvae, 1975-77 251
mackerel, Atlantic
spawning and fecundity 103

Atlantic Ocean
tuna, bluefin
shedding rates of plastic and metal dart tags 179

Atlantic Ocean, eastern
sailfish
size and possible origin 805

Atlantic Ocean, Middle region
mackerel, Atlantic
1978 spring recreational catch 799

Atlantic Ocean, northwest
fishes
organochlorine residues 51

Atlantic Ocean, western North
dolphin, Atlantic whitesided
southern distribution 167

BAGLIN, RAYMOND E., JR., MARK I. FARBER, WILLIAM H. LENARZ, and JOHN M. MASON, JR., "Shedding rates of plastic and metal dart tags from Atlantic bluefin tuna, *Thunnus thynnus*" 179

BAILEY, JACK E.—see RICE and BAILEY

BAILEY, JACK E., STANLEY D. RICE, JEROME J. PELLA, and SIDNEY G. TAYLOR, "Effects of seeding density of pink salmon, *Oncorhynchus gorbuscha*, eggs on water chemistry, fry characteristics, and fry survival in gravel incubators" 649

Bairdiella chrysoura—see Perch, silver

Balaena mysticetus—see Whale, bowhead

BAUCOM, JOE—see ODELL et al.

BEARDSLEY, GRANT L., "Size and possible origin of sailfish, *Istiophorus platypterus*, from the eastern Atlantic Ocean" 805

BENIRSCHKE, K., MARY L. JOHNSON, and ROLF J. BENIRSCHKE, "Is ovulation in dolphins, *Stenella longirostris* and *Stenella attenuata*, always copulation-induced?" 507

BENIRSCHKE, ROLF J.—see BENIRSCHKE et al.

Bering Sea
whale, bowhead
estimated initial population size of stock 843

Bering Sea, eastern
Psychrolutes phrictus
additional records 169

Bikini, Marshall Islands
ciguatera survey 201

BISHOP, JAMES M., JAMES G. GOSSELINK, and JAMES H. STONE, "Oxygen consumption and hemolymph osmolality of brown shrimp, *Penaeus aztecus*" ... 741

Blacksmith
influence of water currents and zooplankton densities on daily foraging movements
distribution patterns 837
foraging at incurrent end of reef 838
foraging experiments 831, 835
physical measurements 832
plankton sampling 831
study site 830
surveys 830
zooplankton distribution patterns 839

BLAYLOCK, J. W.—see PEARSON et al.

"Bomolochid copepods parasitic on the eyes of Indo-West Pacific clupeid fishes," by Roger Cressey and Hillary Boyle Cressey 715

BORDEN, DAVID V. D.—see FOGARTY et al.

Box-Jenkins models
using to forecast fishery dynamics 887

BRANSTETTER, STEVEN, and ROBERT L. SHIPP, "Occurrence of the finetooth shark, *Carcharhinus isodon*, off Dauphin Island, Alabama" 177

BRAY, RICHARD N., "Influence of water currents and zooplankton densities on daily foraging movements of blacksmith, *Chromis punctipinnis*, a planktivorous reef fish" 829

BRAY, RICHARD N.—see EBELING et al.

BREIWICK, JEFFREY M., EDWARD D. MITCHELL, and DOUGLAS G. CHAPMAN, "Estimated initial population size of the Bering Sea stock of bowhead whale, *Balaena mysticetus*: An iterative method" 843

Brevoortia patronus—see Menhaden, Gulf

Brevoortia tyrannus—see Menhaden, Atlantic

BULLARD, FERN A., and JEFF COLLINS, "An improved method to analyze trimethylamine in fish and the interference of ammonia and dimethylamine" 465

Butterfish, Pacific
seasonal spawning cycle 977

California
food of Pacific white-sided dolphin, Dall's porpoise, and northern fur seal off ... 951

California Bight, southern
anchovy, northern
percentage of starving larvae ... 475

Callinectes
larvae in Middle Atlantic Bight, 1975-77
cooccurring decapods ... 259
distribution ... 255
identification ... 254

"*Callinectes* (Decapoda: Portunidae) larvae in the Middle Atlantic Bight, 1975-77," by Peter O. Smyth ... 251

Callinectes sapidus—see Crab, blue

Callorhinus ursinus—see Seal, northern fur

CAMPBELL, DOUGLAS W.—see MILLER et al.

Cancer magister—see Crab, Dungeness

Cape Fear River, North Carolina
fishes, postlarval
retention in an intensively flushed tidal estuary ... 419

Cape Hatteras, North Carolina
croaker, Atlantic
maturity, spawning, and fecundity north of ... 190

Carcharhinus isodon—see Shark, finetooth

Caretta caretta—see Turtle, loggerhead

CAREY, ANDREW G., JR.—see CARNEY and CAREY

CARNEY, ROBERT S., and ANDREW G. CAREY, JR., "Effectiveness of metering wheels for measurement of area sampled by beam trawls" ... 791

CASTAGNA, MICHAEL—see KRAEUTER and CASTAGNA

"Ceratioid anglerfishes of the Philippine Archiepelago, with descriptions of five new species," by Theodore W. Pietsch and Jeffrey A. Seigel ... 379

"Changes in body measurements of larval northern anchovy, *Engraulis mordax*, and other fishes due to handling and preservation," by Gail H. Theilacker ... 685

CHAPMAN, DOUGLAS G.—see BREIWICK et al.

CHENG, LANNA, and ERIC SHULENBERGER, "Distribution and abundance of *Halobates* species (Insecta: Heteroptera) in the eastern tropical Pacific" ... 579

Chesapeake Bay
Squilla empusa
larval ecology ... 693

CHRISTENSEN, DARRYL J., and WALTER J. CLIFFORD, "The 1978 spring recreational catch of Atlantic mackerel, *Scomber scombrus*, off the Middle Atlantic region" ... 799

Chromis punctipinnis—see Blacksmith

Ciguatera
survey at Enewetak and Bikini, Marshall Islands
Acanthuridae ... 240
Balistidae ... 243
Carcharhinidae ... 206
Crangidae ... 233
Dasyatidae ... 211
Holocentridae ... 213
Kyphosidae ... 232
Labridae ... 237
Lethrinidae ... 228
Lutjanidae ... 223
Mugilidae ... 215
Muraenidae ... 212
Orectolobidae ... 205
Scaridae ... 238
Scombridae ... 235
Serranidae ... 216
Sphyraenidae ... 214

Clam, hard
effects of large predators on field culture ... 538

CLARKE, THOMAS A., "Diets of fourteen species of vertically migrating mesopelagic fishes in Hawaiian waters" ... 619

CLAUSEN, DAVID M., "Summer food of Pacific cod, *Gadus macrocephalus*, in coastal waters of southeastern Alaska" ... 968

CLIFFORD, WALTER J.—see CHRISTENSEN and CLIFFORD

Clupeid fishes
Pacific, Indo-West
bomolochid copepods parasitic on eyes ... 715

Cod, Pacific
Alaska, southeastern
summer food ... 968
larval development in northeast Pacific Ocean compared with Pacific tomcod ... 923

COE, JAMES M., and WARREN E. STUNTZ, "Passive behavior by the spotted dolphin, *Stenella attenuata*, in tuna purse seine nets" ... 535

COLLINS, JEFF—see BULLARD and COLLINS

Columbia River
transportation of smolts
salmon, chinook ... 491
steelhead ... 491

"Comparison of sampling devices for the juvenile blue

crab, *Callinectes sapidus*," by Robert E. Miller, Douglas W. Campbell, and Pamela J. Lunsford 196

Copepods, bomolochid
parasitic on eyes of Indo-West Pacific clupeid fishes
Pseudorbitacolax fimbriatus 716
Pseudorbitacolax nudus 724
Pseudorbitacolax Pillai 1971 715
Pseudorbitacolax varunae (Bennet 1966) 720
Pumiliopes jonesi (Bennet 1967) 729
Pumiliopes opisthopteri Shen 1957 729
Pumiliopes Shen 1957 729
Pumiliopes squamosus Cressey and Boyle 1973 730
Pumiliopsis Pillai 1967 724
Pumiliopsis plautus Cressey and Boyle 1973 726
Pumiliopsis sardinellae (Bennet 1964) 726

Copper
effects of an early life history stages of northern anchovy 675

CORNELL, LANNY H.—see ODELL et al.

Coryphaena equiselis
development and structure of fins and fin supports ... 277

Coryphaena hippurus
development and structure of fins and fin supports ... 277

Crab, blue
sampling devices for juvenile, comparison 196

Crab, Dungeness
petroleum hydrocarbon detection by
chemosensory threshold determination 822
composition of water soluble fraction 823
detection thresholds 823
experimental solutions 822

CRESSEY, HILLARY BOYLE—see CRESSEY and CRESSEY

CRESSEY, ROGER, and HILLARY BOYLE CRESSEY, "Bomolochid copepods parasitic on the eyes of Indo-West Pacific clupeid fishes" 715

Croaker, Atlantic
Cape Fear River, North Carolina
retention of postlarval in tidal estuary 419
maturity, spawning, and fecundity north of Cape Hatteras, North Carolina 190

"Daily time of spawning of 12 fishes in the Peconic Bays, New York," by Steven P. Ferraro 455

Dauphin Island, Alabama
shark, finetooth
occurrence off 177

DAVIS, GARY E., "Effects of injuries on spiny lobster, *Panulirus argus*, and implications for fishery management" 979

"Depth distribution and seasonal and diel movements of ratfish, *Hydrolagus colliei*, in Puget Sound, Washington," by Thomas P. Quinn, Bruce S. Miller, and R. Craig Wingert 816

"Descriptions of larval silver perch, *Bairdiella chrysoura*, banded drum, *Larimus fasciatus*, and star drum, *Stellifer lanceolatus* (Sciaenidae)," by Howard Powles .. 119

"Detection of petroleum hydrocarbons by the Dungeness crab, *Cancer magister*," by Walter H. Pearson, Peter C. Sugarman, Dana L. Woodruff, J. W. Blaylock, and Bori L. Olla 821

"Development and structure of fins and fin supports in dolphin fishes *Coryphaena hippurus* and *Coryphaena equiselis* (Coryphaenidae)," by Thomas Potthoff 277

"Development of larval smooth flounder, *Liopsetta putnami*, with a redescription of development of winter flounder, *Pseudopleuronectes americanus* (Family Pleuronectidae)," by Wayne A. Laroche 897

"Diel and seasonal variation in abundance and diversity of shallow-water fish populations in Morrow Bay, California," by Michael H. Horn 759

"Diets of fourteen species of vertically migrating mesopelagic fishes in Hawaiian waters," by Thomas A. Clarke 619

"(A) direct method for estimating northern anchovy, *Engraulis mordax*, spawning biomass," by Keith Parker 541

"Distribution and abundance of *Halobates* species (Insecta: Heteroptera) in the eastern tropical Pacific," by Lanna Cheng and Eric Shulenberger 579

Dolphin, Atlantic whitesided
Atlantic Ocean, western North
southern distribution 167

Dolphin, bottlenose
occurrence, movements, and distribution in southern Texas 593

Dolphin, Pacific white-sided
food of, off California and Washington
prey distribution 955
prey size 957
prey species 955
stomach capacity of predators 955

Dolphin, spinner
is ovulation always copulation-induced?
early pregnancy 512
immature females 508
lactating females 518
late pregnancy 515
mature females 509
nonpregnant animals with corpus luteum 518
observations on mass stranding, west coast of Florida
circumstances 353
morphology, external 358
necropsy 355

physical maturity 358
productive seasonality 357
reproductive data 355
weights 360

Dolphin, spotted
is ovulation always copulation-induced?
early pregnancy 512
immature females 508
lactating females 518
late pregnancy 515
mature females 509
nonpregnant animals with corpus luteum 518
passive behavior in tuna purse seine nets 535

Dolphin fishes
development and structure of fins and fin supports
anal fin 290
anal fin pterygiophores 291
caudal fin 295
caudal fin supports 296
dorsal fin 278
dorsal fin pterygiophores 281
pectoral fin and supports 300
pelvic fin and supports 304
vertebral column 278

Drum, banded
comparison with earlier descriptions 133
comparison with other larval Sciaenidae 134
description 125
spawning seasons and areas 133

Drum, star
comparison with earlier descriptions 133
comparison with other larval Sciaenidae 134
description 129
spawning seasons and areas 134

DUNN, JEAN R.—see MATARESE et al.

DUNN, JEAN R.—see RICHARDSON et al.

DURBIN, ANN G., EDWARD G. DURBIN, PETER G. VERITY, and THOMAS J. SMAYDA, "Voluntary swimming speeds and respiration rates of a filter-feeding planktivore, the Atlantic menhaden, *Brevoortia tyrannus* (Pisces: Clupeidae)" 877

DURBIN, EDWARD G.—see DURBIN et al.

"Early life history of Pacific mackerel, *Scomber japonicus*," by John R. Hunter and Carol A. Kimbrell 89

EBEL, WESLEY J., "Transporation of chinook salmon, *Oncorhynchus tshawytscha*, and steelhead, *Salmo gairdneri*, smolts in the Columbia River and effects on adult returns" 491

EBELING, ALFRED W., RALPH J. LARSON, WILLIAM S. ALEVIZON, and RICHARD N. BRAY, "Annual variability of reef-fish assemblages in kelp forests off Santa Barbara, California" 361

"Effect of zinc on fin regeneration in the mummichog, *Fundulus heteroclitus*, and its interaction with methylmercury," by Peddrick Weis and Judith Shulman Weis . 163

"Effectiveness of metering wheels for measurement of area sampled by beam trawls," by Robert S. Carney and Andrew G. Carey, Jr. 791

"Effects of copper on early life history stages of northern anchovy, *Engraulis mordax*," by D. W. Rice, Jr., F. L. Harrison, and A. Jearld, Jr. 675

"Effects of injuries on spiny lobster, *Panulirus argus*, and implications for fishery management," by Gary E. Davis 979

"Effects of large predators on the field culture of the hard clam, *Mercenaria mercenaria*," by John N. Kraeuter and Michael Castagna 538

"Effects of seeding density of pink salmon, *Oncorhynchus gorbuscha*, eggs on water chemistry, fry characteristics, and fry survival in gravel incubators," by Jack E. Bailey, Stanley D. Rice, Jerome J. Pella, and Sidney G. Taylor 649

"Egg and larval development of the spot, *Leiostomus xanthurus* (Sciaenidae)," by Allyn B. Powell and Herbert R. Gordy 701

"Egg cannibalism in the northern anchovy, *Engraulis mordax*," by John R. Hunter and Carol A. Kimbrell 811

"Eggs and larvae of butter sole, *Isopsetta isolepis* (Pleuronectidae), off Oregon and Washington," by Sally L. Richardson, Jean R. Dunn, and Nancy Anne Naplin . 401

Enewetak, Marshall Islands
ciguatera survey 201

Engraulis mordax—see Anchovy, northern

Enhydra lutris—see Otter, sea

"Estimated initial population size of the Bering Sea stock of bowhead whale, *Balaena mysticetus*: An iterative method," by Jeffrey M. Breiwick, Edward D. Mitchell, and Douglas G. Chapman 843

Euphausia eximia
larval development
distribution, vertical 331
larval stages described 315
observations of reared animals 315
population, South Pacific 328

"Factors controlling growth and survival of cultured spot prawn, *Pandalus platyceros*, in Puget Sound, Washington," by John E. Rensel and Earl F. Prentice 781

Farallon Islands
pinnipeds
predation by sharks 941

FARBER, MARK I.—see BAGLIN et al.

"Feeding ecology of *Lagodon rhomboides* (Pisces: Sparidae): Variation and functional responses," by Allan W. Stoner 337

FERRARO, STEVEN P., "Daily time of spawning of 12 fishes in the Peconic Bays, New York" 455

FISCUS, CLIFFORD H.—see STROUD et al.

Fish
trimethylamine
improved method to analyze, and interference of ammonia and dimethylamine 465

Fish assemblages, reef
annual variability in kelp forest off Santa Barbara, California
cinetransects 363
sampling 372
spatial differences 365
statistical analyses 364
study sites 362
yearly differences 369, 373

Fish larvae
anchovy, northern
percentage of starving in southern California Bight 475

Fish meal
demand model for United States
functional form 270
lagged response mechanisms 271
simultaneity bias 270
specification 268
statistical procedures 272

Fish populations
diel and seasonal variation in abundance and diversity of shallow-water, in Morrow Bay, California 759
multistage recruitment process for laboratory
data collection 558
experimental design 559
experimental environments 557
feeding 558
marking 558
mathematical model, development 569
phase I 561
phase II 566

Fishery dynamics
using Box-Jenkins models to forecast
data and underlying model 888
estimation and checking 891
forecasts 893
model identification 890
transfer function models 892

Fishes
Atlantic Ocean, northwest, and Gulf of Mexico
organochlorine residues 51
daily time of spawning in the Peconic Bays, New York 455
seasonality of, occupying surf zone habitat in Gulf of Mexico
annual and seasonal occurrence 913
daily activity patterns 916
factors affecting occurrence 920
seasonal and annual variations 918
species composition 918

Fishes, marine
life history patterns and consequences for fisheries management
r and *K* selection 2
response of *r* and *K* selected species to harvesting . 4
theory of *r* and *K* selection 1

Fishes, mesopelagic
diets of vertically migrating in Hawaiian waters
Benthosema suborbitale 630
Bolinichthys longipes 629
Bregmaceros japonicus 632
Ceratoscopelus warmingi 628
Diaphus fragilis 632
Diaphus perspicillatus 631
Diaphus schmidti 630
Diaphus trachops 632
Diogenichthys atlanticus 630
field collections 619
laboratory procedures 620
Lampanyctus nobilis 623
Lampanyctus steinbecki 623
Melamphaes danae 632
Notolychnus valdiviae 628
Triphoturus nigrescens 625

Fishes, postlarval
retention of three taxa in tidal estuary, Cape Fear River, North Carolina
behavior, diel 423
length-frequency distributions 429
tide response 426

Florida
whale, false killer
recurrent mass stranding 171

Florida, west coast
dolphin, spinner
observations of mass stranding 353

Flounder, smooth
development of larval with redescription of development of winter flounder
distinguishing features 900
fin development 902
general development 900
identification 898
laboratory observations 899
morphology 901
pigmentation 903
terminology 898

Flounder, winter
redescription of development 897

Flounder, yellowtail
temperature effects on growth and yolk utilization in yolk-sac larvae 731

FOGARTY, MICHAEL J., DAVID V. D. BORDEN, and HOWARD J. RUSSELL, "Movements of tagged American lobster, *Homarus americanus*, off Rhode Island" ... 771

"Food of the Pacific white-sided dolphin, *Lagenorhynchus obliquidens*, Dall's porpoise, *Phocoenoides dalli*, and northern fur seal, *Callorhinus ursinus*, off California and Washington," by Richard K. Stroud, Clifford H. Fiscus, and Hiroshi Kajimura ... 951

"Food of the harbor seal, *Phoca vitulina richardsi*, in the Gulf of Alaska," by Kenneth W. Pitcher ... 549

Fundulus heteroclitus—see Mummichog

Gadus macrocephalus—see Cod, Pacific

GERRY, LAWRENCE R.—see WEINSTEIN et al.

GOLDBERG, STEPHEN R., "Seasonal spawning cycle of the Pacific butterfish, *Peprilus simillimus* (Stromateidae)" ... 977

GORDY, HERBERT R.—see POWELL and GORDY

GOSSELINK, JAMES G.—see BISHOP et al.

GRAY, ROBERT J.—see HAYNES and GRAY

GRIMES, CHURCHILL B., and GENE R. HUNTSMAN, "Reproductive biology of the vermilion snapper, *Rhomboplites aurorubens*, from North Carolina and South Carolina" ... 137

GRISWOLD, CAROLYN A., and JEROME PREZIOSO, "In situ observations on reproductive behavior of the long-finned squid, *Loligo pealei*" ... 945

Gulf of Alaska
  seal, harbor
    food of ... 549
    stomach contents and feces as indicators of foods .. 797

Gulf of Mexico
  fishes
    organochlorine residues ... 51
  shrimp fishery
    use of Griffin's yield model ... 973

Gulf of Mexico, northern
  fishes
    seasonality of, occupying surf zone habitat ... 911

Halobates species
  distribution and abundance in eastern tropical Pacific
    cooccurrence ... 589
    temperature effects ... 589

HANKIN, DAVID G., "A multistage recruitment process in laboratory fish populations: Implications for models of fish population dynamics" ... 555

HARRISON, F. L.—see RICE et al.

Hawaii
  fishes, mesopelagic
    diets of vertically migrating ... 619

HAYNES, JAMES M., and ROBERT H. GRAY, "Influence of Little Goose Dam on upstream movements of adult chinook salmon, *Oncorhynchus tshawytscha*" .. 185

HINES, ANSON H., and THOMAS R. LOUGHLIN, "Observations of sea otters digging for clams at Monterey Harbor, California" ... 159

HODSON, RONALD G.—see WEINSTEIN et al.

Homarus americanus—see Lobster, American

HORN, MICHAEL H., "Diel and seasonal variation in abundance and diversity of shallow-water fish populations in Morrow Bay, California" ... 759

HOWELL, W. HUNTTING, "Temperature effects on growth and yolk utilization in yellowtail flounder, *Limanda ferruginea*, yolk-sac larvae" ... 731

HUBER, HARRIET R.—see AINLEY et al.

HULBERG, LARRY W.—see OLIVER et al.

HUNTER, JOHN R., and CAROL A. KIMBRELL, "Early life history of Pacific mackerel, *Scomber japonicus*" ... 89

HUNTER, JOHN R., and CAROL A. KIMBRELL, "Egg cannibalism in the northern anchovy, *Engraulis mordax*" ... 811

HUNTSMAN, GENE R.—see GRIMES and HUNTSMAN

HUPPERT, D. D., "An analysis of the United States demand for fish meal" ... 267

Hydrolagus colliei—see Ratfish

"(An) improved method to analyze trimethylamine in fish and the interference of ammonia and dimethylamine," by Fern A. Bullard and Jeff Collins ... 465

"In situ observations on reproductive behavior of the long-finned squid, *Loligo pealei*," by Carolyn A. Griswold and Jerome Prezioso ... 945

Incubators, gravel
  effects of seeding density of pink salmon eggs on water chemistry and fry characteristics and survival ... 649

"Influence of Little Goose Dam on upstream movements of adult chinook salmon, *Oncorhynchus tshawytscha*," by James M. Haynes and Robert H. Gray ... 185

"Influence of water currents and zooplankton densities on daily foraging movements of blacksmith, *Chromis punctipinnis*, a planktivorous reef fish," by Richard N. Bray ... 829

Invertebrate communities, benthic
relationships between wave disturbance and zonation in Monterey Bay, California
canyon ridge transect 448
crustacean zone 443
environmental setting 439
polychaete zone 446
sandflat, northern 447
seasonal patterns 449

"Is ovulation in dolphins, *Stenella longirostris* and *Stenella attenuata*, always copulation-induced?," by K. Benirschke, Mary L. Johnson, and Rolf J. Benirschke 507

Isopsetta isolepis—see Sole, butter

Istiophorus platypterus—see Sailfish

JEARLD, A., JR.—see RICE et al.

JOHANSEN, P. H.—see PETERSON et al.

JOHNSON, JAMES H., "Production and growth of subyearling coho salmon, *Oncorhynchus kisutch*, chinook salmon, *Oncorhynchus tshawytscha*, and steelhead, *Salmo gairdneri*, in Orwell Brook, tributary of Salmon River, New York" 549

JOHNSON, MARY L.—see BENIRSCHKE et al.

KAJIMURA, HIROSHI—see STROUD et al.

KHILNANI, ARVIND, "Use of Griffin's yield model for the Gulf of Mexico shrimp fishery" 973

KIMBRELL, CAROL A.—see HUNTER and KIMBRELL

KNIGHT, MARGARET D., "Larval development of *Euphausia eximia* (Crustacea: Euphausiacea) with notes on its vertical distribution and morphological divergence between populations" 313

KRAEUTER, JOHN N., and MICHAEL CASTAGNA, "Effects of large predators on the field culture of the hard clam, *Mercenaria mercenaria*" 538

Lagenorhynchus acutus—see Dolphin, Atlantic white-sided

Lagenorhynchus obliquidens—see Dolphin, Pacific white-sided

Lagodon rhomboides—see Pinfish

"(A) large, opening-closing midwater trawl for sampling oceanic nekton, and comparison of catches with an Isaacs-Kidd midwater trawl," by William G. Pearcy 529

Larimus fasciatus—see Drum, banded

LAROCHE, JOANNE LYCZKOWSKI, and SALLY L. RICHARDSON, "Reproduction of northern anchovy, *Engraulis mordax*, off Oregon and Washington" 603

LAROCHE, WAYNE A., "Development of larval smooth flounder, *Liopsetta putnami*, with a redescription of development of winter flounder, *Pseudopleuronectes americanus* (Family Pleuronectidae)" 897

LARSON, RALPH J.—see EBELING et al.

Larvae, fish—see Fish larvae

"Larval development of *Euphausia eximia* (Crustacea: Euphausiacea) with notes on its vertical distribution and morphological divergence between populations," by Margaret D. Knight 313

"Larval development of Pacific tomcod, *Microgadus proximus*, in the northeast Pacific Ocean with comparative notes on larvae of walleye pollock, *Theragra chalcogramma*, and Pacific cod, *Gadus macrocephalus* (Gadidae)," by Ann C. Matarese, Sally L. Richardson, and Jean R. Dunn 923

Leiostomus xanthurus—see Spot

LENARZ, WILLIAM H.—see BAGLIN et al.

LENARZ, WILLIAM H., and PETER B. ADAMS, "Some statistical considerations of the design of trawl surveys for rockfish (Scorpaenidae)" 659

LEONG, J. K.—see McLELLAN and LEONG

Lepidochelys kempi—see Turtle, Atlantic ridley

LEWIS, ROBERT M., and CHARLES M. ROITHMAYR, "Spawning and sexual maturity of Gulf menhaden, *Brevoortia patronus*" 947

LEWIS, T. JAMES—see AINLEY et al.

"Life history patterns in marine fishes and their consequences for fisheries management," by Peter B. Adams 1

Limanda ferruginea—see Flounder, yellowtail

Liopsetta putnami—see Flounder, smooth

Lobster, American
movements of tagged off Rhode Island 771

Lobster, spiny
effects of injuries and implications for fishery management 979

Loligo pealei—see Squid, long-finned

LOUGHLIN, THOMAS R.—see HINES and LOUGHLIN

LUNSFORD, PAMELA J.—see MILLER et al.

Mackerel, Atlantic
Middle Atlantic region, 1978 spring recreational catch
catch rate estimation 801
fishing effort estimation 800

lengths, weights, and age composition 802
sampling 799
spawning and fecundity in Middle Atlantic Bight 103
voluntary swimming speeds and respiration rates
experimental procedure 878
feeding measurements 882
initial and final measurements 881
postfeeding measurements 882

Mackerel, jack
rearing container size affects morphology and nutritional condition of larval 789

Mackerel, Pacific
life history, early
feeding behavior 94
growth 93
hatching, onset of feeding, and starvation 91
laboratory experiments and sea samples 89
larvae culture 91
ration, growth efficiency, and metabolism 97
swimming behavior 94

Markov decision models
using, and related techniques for purposes other than simple optimization
defining the model on a discrete grid 37
model 36
policy analysis 39

MARLIAVE, JEFFREY B., "Spawn and larvae of the Pacific sandfish, *Trichodon trichodon*" 959

MASON, JOHN M., JR.—see BAGLIN et al.

MATARESE, ANN C., SALLY L. RICHARDSON, and JEAN R. DUNN, "Larval development of Pacific tomcod, *Microgadus proximus*, in the northeast Pacific Ocean with comparative notes on larvae of walleye pollock, *Theragra chalcogramma*, and Pacific cod, *Gadus macrocephalus* (Gadidae)" 923

MATARESE, ANN C., and DAVID L. STEIN, "Additional records of the sculpin *Psychrolutes phrictus* in the eastern Bering Sea and off Oregon" 169

"Maturity, spawning, and fecundity of Atlantic croaker, *Micropogonias undulatus*, occurring north of Cape Hatteras, North Carolina," by Wallace W. Morse 190

McLELLAN, G. L., and J. K. LEONG, "A radiologic method for examination of the gastrointestinal tract in the Atlantic ridley, *Lepidochelys kempi*, and loggerhead, *Caretta caretta*, marine turtles" 965

MEAD, JAMES G.—see TESTAVERDE and MEAD

MEAD, JAMES G., DANIEL K. ODELL, RANDALL S. WELLS, and MICHAEL D. SCOTT, "Observations on a mass stranding of spinner dolphin, *Stenella longirostris*, from the west coast of Florida" 353

MENDELSSOHN, ROY, "Using Box-Jenkins models to forecast fishery dynamics: Identification, estimation, and checking" 887

MENDELSSOHN, ROY, "Using Markov decision models and related techniques for purposes other than simple optimization: Analyzing the consequences of policy alternatives on the management of salmon runs" 35

Menhaden, Gulf
spawning and sexual maturity
age and size of first spawning 948
ova spawned, number 950
stages of sexual maturity 948
time and frequency of spawning 949

Mercenaria mercenaria—see Clam, hard

METCALFE, J. L.—see PETERSON et al.

Microgadus proximus—see Tomcod, Pacific

Microgadus tomcod—see Tomcod, Atlantic

Micropogonias undulatus—see Croaker, Atlantic

MILLER, BRUCE S.—see QUINN et al.

MILLER, ROBERT E., DOUGLAS W. CAMPBELL, and PAMELA J. LUNSFORD, "Comparison of sampling devices for the juvenile blue crab, *Callinectes sapidus*" ... 196

MITCHELL, EDWARD D.—see BREIWICK et al.

MODDE, TIMOTHY, and STEPHEN T. ROSS, "Seasonality of fishes occupying a surf zone habitat in the northern Gulf of Mexico" 911

Monterey Bay, California
invertebrate community, benthic
relationships between wave disturbance and zonation along a subtidal high-energy beach 437

Monterey Harbor, California
otter, sea
observations on digging for clams 159

MORGAN, STEVEN G., "Aspects of larval ecology of *Squilla empusa* (Crustacea, Stomatopoda) in Chesapeake Bay" 693

MORRELL, STEPHEN H.—see AINLEY et al.

Morro Bay, California
fish populations, shallow-water
diel and seasonal variation in abundance and diversity 759

MORSE, WALLACE W., "Maturity, spawning, and fecundity of Atlantic croaker, *Micropogonias undulatus*, occurring north of Cape Hatteras, North Carolina" 190

MORSE, WALLACE W., "Spawning and fecundity of Atlantic mackerel, *Scomber scombrus*, in the Middle Atlantic Bight" 103

"Movements of tagged American lobster, *Homarus americanus*, off Rhode Island," by Michael J. Fogarty, David V. D. Borden, and Howard J. Russell 771

"(A) multistage recruitment process in laboratory fish populations: Implications for models of fish population dynamics," by David G. Hankin 555

Mummichog
fin regeneration
effect of zinc on and its interaction with methylmercury 163

Munidopsis
species occurring off Oregon and adjacent waters
characters of taxonomic importance 16
key to species 16
Munidopsis aries 17
Munidopsis bairdii 18
Munidopsis beringana 24
Munidopsis cascadia n. sp. 21
Munidopsis ciliata 19
Munidopsis latirostris 28
Munidopsis quadrata 17
Munidopsis sp. 18
Munidopsis subsquamosa 26
Munidopsis tuftsi n. sp. 24
Munidopsis verrucosus 27
Munidopsis yaquinensis n. sp. 20
vertical and geographic distribution 29

NAPLIN, NANCY ANNE—see RICHARDSON et al.

Nekton, oceanic
opening-closing midwater trawl vs. Isaacs-Kidd midwater trawl 529

Nets
tuna purse seine
passive behavior of spotted dolphins 535

"(The) 1978 spring recreational catch of Atlantic mackerel, *Scomber scombrus*, off the Middle Atlantic region," by Darryl J. Christensen and Walter J. Clifford 799

North Carolina
snapper, vermilion
reproductive biology 137

NYBAKKEN, JAMES W.—see OLIVER et al.

"Observations of sea otters digging for clams at Monterey Harbor, California," by Anson H. Hines and Thomas R. Loughlin 159

"Observations on a mass stranding of spinner dolphin, *Stenella longirostris*, from the west coast of Florida," by James G. Mead, Daniel K. Odell, Randall S. Wells, and Michael D. Scott 353

"Observations on early life stages of Atlantic tomcod, *Microgadus tomcod*," by R. H. Peterson, P. H. Johansen, and J. L. Metcalfe 147

"Occurrence, movements, and distribution of bottlenose dolphin, *Tursiops truncatus*, in southern Texas," by Susan H. Shane 593

"Occurrence of the finetooth shark, *Carcharhinus isodon*, off Dauphin Island, Alabama," by Steven Branstetter and Robert L. Shipp 177

O'CONNELL, CHARLES P., "Percentage of starving northern anchovy, *Engraulis mordax*, larvae in the sea as estimated by histological methods" 475

ODELL, DANIEL K.—see MEAD et al.

ODELL, DANIEL K., EDWARD D. ASPER, JOE BAUCOM, and LANNY H. CORNELL, "A recurrent mass stranding of the false killer whale, *Pseudorca crassidens*, in Florida" 171

OLIVER, JOHN S., PETER N. SLATTERY, LARRY W. HULBERG, and JAMES W. NYBAKKEN, "Relationships between wave disturbance and zonation of benthic invertebrate communities along a subtidal high-energy beach in Monterey Bay, California" 437

OLLA, BORI L.—see PEARSON et al.

Oncorhynchus gorbuscha—see Salmon, pink

Oncorhynchus kisutch—see Salmon, coho

Oncorhynchus tshawytscha—see Salmon, chinook

Oregon
anchovy, northern
reproduction off 603
spawning biomass and early life in northern subpopulation 855
Psychrolutes phrictus
additional records 169
sole, butter
eggs and larvae off 401

Organochlorine residues
fishes, northwest Atlantic Ocean and Gulf of Mexico . 51

"Organochlorine residues in fishes from the northwest Atlantic Ocean and Gulf of Mexico," by Virginia F. Stout 51

Orwell Brook, New York
production and growth of subyearling
salmon, chinook 549
salmon, coho 549
steelhead 549

Otter, sea
Monterey Harbor, California
observations on digging for clams 159

"Oxygen consumption and hemolymph osmolality of brown shrimp, *Penaeus aztecus*," by James M. Bishop, James G. Gosselink, and James H. Stone 741

Pacific Ocean, eastern North
anglerfishes, ceratioid
description of new species 59

Pacific Ocean, eastern tropical
Halobates species
distribution and abundance 579

Pacific Ocean, Indo-West
clupeid fishes
bomolochid copepods parasitic on eyes of 716

Pacific Ocean, northeast
tomcod, Pacific
larval development 923

Pandalus platyceros—see Prawn, spot

Panulirus argus—see Lobster, spiny

PARKER, KEITH, "A direct method for estimating northern anchovy, *Engraulis mordax*, spawning biomass" 541

"Passive behavior by the spotted dolphin, *Stenella attenuata*, in tuna purse seine nets," by James M. Coe and Warren E. Stuntz 535

PEARCY, WILLIAM G., "A large, opening-closing midwater trawl for sampling oceanic nekton, and comparison of catches with an Isaacs-Kidd midwater trawl" ... 529

PEARSON, WALTER H., PETER C. SUGARMAN, DANA L. WOODRUFF, J. W. BLAYLOCK, and BORI L. OLLA, "Detection of petroleum hydrocarbons by the Dungeness crab, *Cancer magister*" 821

Peconic Bays, New York
fish spawning, daily time of 455

PELLA, JEROME J.—see BAILEY et al.

Penaeus aztecus—see Shrimp, brown

Peprilus simillimus—see Butterfish, Pacific

"Percentage of starving northern anchovy, *Engraulis mordax*, larvae in the sea as estimated by histological methods," by Charles P. O'Connell 475

Perch, silver
comparison with earlier descriptions 132
comparison with other larval Sciaenidae 134
description 122
spawning seasons and areas 133

PETERSON, R. H., P. H. JOHANSEN, and J. L. METCALFE, "Observations on early life stages of Atlantic tomcod, *Microgadus tomcod*" 147

Philippine Archipelago
anglerfishes, ceratioid
descriptions of five new species 379

Phoca vitulina—see Seal, harbor

Phoca vitulina richardsi—see Seal, harbor

Phocoenoides dalli—see Porpoise, Dall's

PIETSCH, THEODORE W., and JEFFREY A. SIEGEL, "Ceratioid anglerfishes of the Philippine Archipelago, with descriptions of five new species" 379

PIETSCH, THEODORE W., and JOHN P. VAN DUZER, "Systematics and distribution of ceratioid anglerfishes of the family Melanocetidae with the description of a new species from the eastern North Pacific Ocean" 59

Pinfish
feeding ecology
variation and functional responses 337

Pinnipeds
predation by sharks at Farallon Islands 941

PITCHER, KENNETH W., "Food of the harbor seal, *Phoca vitulina richardsi*, in the Gulf of Alaska" 549

PITCHER, KENNETH W., "Stomach contents and feces as indicators of harbor seal, *Phoca vitulina*, foods in the Gulf of Alaska" 797

Pollock, walleye
larval development in northeast Pacific Ocean
compared with Pacific tomcod 923

Porpoise, Dall's
food of, off California and Washington
prey distribution 955
prey size 957
prey species 955
stomach capacity of predators 955

POTTHOFF, THOMAS, "Development and structure of fins and fin supports in dolphin fishes *Coryphaena hippurus* and *Coryphaena equiselis* (Coryphaenidae)" .. 277

POWELL, ALLYN B., and HERBERT R. GORDY, "Egg and larval development of the spot, *Leiostomus xanthurus* (Sciaenidae)" 701

POWLES, HOWARD, "Descriptions of larval silver perch, *Bairdiella chrysoura*, banded drum, *Larimus fasciatus*, and star drum, *Stellifer lanceolatus* (Sciaenidae)" 119

Prawn, spot
factors controlling growth and survival of cultured in Puget Sound, Washington
environmental data 783
juveniles 783
molting 785
yearlings 785

"Predation by sharks on pinnipeds at the Farallon Islands," by David G. Ainley, Craig S. Strong, Harriet R. Huber, T. James Lewis, and Stephen H. Morrell 941

PRENTICE, EARL F.—see RENSEL and PRENTICE

PREZIOSO, JEROME—see GRISWOLD and PREZIOSO

"Production and growth of subyearling coho salmon, *Oncorhynchus kisutch*, chinook salmon, *Oncorhynchus tshawytscha*, and steelhead, *Salmo gairdneri*, in Orwell Brook, tributary of Salmon River, New York," by James H. Johnson 549

Pseudopleuronectes americanus—see Flounder, winter

Pseudorca crassidens—see Whale, false killer

Psychrolutes phrictus
additional records from eastern Bering Sea and off Oregon 169

Puget Sound, Washington
prawn, spot
factors controlling growth and survival of cultured 781
ratfish
depth distribution and seasonal diel movements ... 816

QUINN, THOMAS P., BRUCE S. MILLER, and R. CRAIG WINGERT, "Depth distribution and seasonal and diel movements of ratfish, *Hydrolagus colliei*, in Puget Sound, Washington" 816

"(A) radiologic method for examination of the gastrointestinal tract in the Atlantic ridley, *Lepidochelys kempi*, and loggerhead, *Caretta caretta*, marine turtles," by G. L. McLellan and J. K. Leong 965

RANDALL, JOHN E., "A survey of ciguatera at Enewetak and Bikini, Marshall Islands, with notes on the systematics and food habits of ciguatoxic fishes" 201

Ratfish
Puget Sound, Washington
depth distribution and seasonal and diel movements 816

"Rearing container size affects morphology and nutritional condition of larval jack mackerel, *Trachurus symmetricus*," by Gail H. Theilacker 789

"(A) recurrent mass stranding of the false killer whale, *Pseudorca crassidens*, in Florida," by Daniel K. Odell, Edward D. Asper, Joe Baucom, and Lanny H. Cornell .. 171

"Relationships between wave disturbance and zonation of benthic invertebrate communities along a subtidal high-energy beach in Monterey Bay, California," by John S. Oliver, Peter N. Slattery, Larry W. Hulberg, and James W. Nybakken 437

RENSEL, JOHN E., and EARL F. PRENTICE, "Factors controlling growth and survival of cultured spot prawn, *Pandalus platyceros*, in Puget Sound, Washington" 781

"Reproduction of northern anchovy, *Engraulis mordax*, off Oregon and Washington," by Joanne Lyczkowski Laroche and Sally L. Richardson 603

"Reproductive biology of the vermilion snapper, *Rhomboplites aurorubens*, from North Carolina and South Carolina," by Churchill B. Grimes and Gene R. Huntsman . 137

"Respiration and depth control as possible reasons for swimming of northern anchovy, *Engraulis mordax*, yolksac larvae," by Daniel Weihs 109

"Retention of three taxa of postlarval fishes in an intensively flushed tidal estuary, Cape Fear River, North Carolina," by Michael P. Weinstein, Sidney L. Weiss, Ronald G. Hodson, and Lawrence R. Gerry 419

Rhode Island
lobster, American
movements of tagged off 771

Rhomboplites aurorubens—see Snapper, vermilion

RICE, D. W., JR., F. L. HARRISON, and A. JEARLD, JR., "Effects of copper on early life history stages of northern anchovy, *Engraulis mordax*" 675

RICE, STANLEY D.—see BAILEY et al.

RICE, STANLEY D., and JACK E. BAILEY, "Ammonia concentrations in pink salmon, *Oncorhynchus gorbuscha*, redds of Sashin Creek, southeastern Alaska" 809

RICE, STANLEY D., and JACK E. BAILEY, "Survival, size, and emergence of pink salmon, *Oncorhynchus gorbuscha*, alevins after short- and long-term exposures to ammonia" 641

RICHARDSON, SALLY L., "Spawning biomass and early life of northern anchovy, *Engraulis mordax*, in the northern subpopulation off Oregon and Washington" .. 855

RICHARDSON, SALLY L.—see LAROCHE and RICHARDSON

RICHARDSON, SALLY L.—see MATARESE et al.

RICHARDSON, SALLY L., JEAN R. DUNN, and NANCY ANNE NAPLIN, "Eggs and larvae of butter sole, *Isopsetta isolepis* (Pleuronectidae), off Oregon and Washington" 401

Rockfish
trawl surveys, statistical considerations of design
comparisons of random, stratified random, and systematic sampling 660
examination of trade offs between tow length and number of tows 667

ROITHMAYR, CHARLES M.—see LEWIS and ROITHMAYR

ROSS, STEPHEN T.—see MODDE and ROSS

RUSSELL, HOWARD J.—see FOGARTY et al.

Sailfish
size and possible origin from eastern Atlantic Ocean . 805

Salmo gairdneri—see Steelhead

Salmon, chinook
influence of Little Goose Dam on upstream movements of adult ... 185
production and growth of subyearling in Orwell Brook, New York ... 549
smolts, transportation in Columbia River and effects on adult returns
collection and marketing of fish and fish hauling procedures ... 493
comparison of results with other studies ... 502
effect of transportation on homing ... 503
evaluation of returning adults ... 494
experimental design ... 493
factors influencing assessment of data ... 494
percentage adult returns of transported releases ... 498
recovery of marked in commercial and sport fisheries ... 500
returns of adult experimental fish to hatcheries and spawning grounds ... 501
returns of adult experimental fish to Little Goose Dam ... 496
size and years-in-ocean of adult experimental fish ... 500
straying of experimental groups ... 502
timing of adult returns ... 499

Salmon, coho
production and growth of subyearling in Orwell Brook, New York ... 549

Salmon, pink
effects of seeding density of eggs on water chemistry and fry characteristics and survival in gravel incubators
dissolved oxygen ... 652
quantity and quality of fry produced ... 653
temperature, pH, and total ammonia in effluent ... 650
water quality and fry production ... 655
Sashin Creek, southeastern Alaska
ammonia concentrations in redds ... 809
survival, size, and emergence of alevins after exposure to ammonia
early emergence ... 644
effect of long-term exposures on fry size at emergence ... 644
sensitivity of different life stages ... 643

Sandfish, Pacific
spawn and larvae
larval development ... 961
life history notes ... 959

Santa Barbara, California
fish assemblages, reef
annual variability in kelp forests off ... 361

Sashin Creek, southeastern Alaska
salmon, pink
ammonia concentrations in redds ... 809

Scomber japonicus—see Mackerel, Pacific

Scomber scombrus—see Mackerel, Atlantic

SCOTT, MICHAEL D.—see MEAD et al.

Seal, harbor
food of, in Gulf of Alaska ... 549
Gulf of Alaska
stomach contents and feces as indicators of foods ... 797

Seal, northern fur
food of, off California and Washington
prey distribution ... 955
prey size ... 957
prey species ... 955
stomach capacity of predators ... 955

"Seasonal spawning cycle of the Pacific butterfish, *Peprilus simillimus* (Stromateidae)," by Stephen R. Goldberg ... 977

"Seasonality of fishes occupying a surf zone habitat in the northern Gulf of Mexico," by Timothy Modde and Stephen T. Ross ... 911

SEIGEL, JEFFREY A.—see PIETSCH and SEIGEL

SHANE, SUSAN H., "Occurrence, movements, and distribution of bottlenose dolphin, *Tursiops truncatus*, in southern Texas" ... 593

Shark, finetooth
occurrence off Dauphin Island, Alabama ... 177

Sharks
Farallon Islands
predation on pinnipeds ... 941

"Shedding rates of plastic and metal dart tags from Atlantic bluefin tuna, *Thunnus thynnus*," by Raymond E. Baglin, Jr., Mark I. Farber, William H. Lenarz, and John M. Mason, Jr. ... 179

SHIPP, ROBERT L.—see BRANSTETTER and SHIPP

Shrimp, brown
oxygen consumption and hemolymph osmolality
crowding effects ... 743, 745
disturbance effects ... 743, 745
diurnal effects ... 743, 744
energy considerations ... 752
reduced-light effects ... 743, 745
salinity effects ... 744, 745, 749
size effects ... 744, 746, 750
temperature effects ... 744, 745, 751
variability sources ... 746

Shrimp fishery
use of Griffin's yield model for Gulf of Mexico
expected value of yield ... 974
parameter sensitivity test ... 975

SHULENBERGER, ERIC—see CHENG and SHULENBERGER

"Size and possible origin of sailfish, *Istiophorus platypterus*, from the eastern Atlantic Ocean," by Grant

L. Beardsley 805

SLATTERY, PETER N.—see OLIVER et al.

SMAYDA, THOMAS J.—see DURBIN et al.

SMYTH, PETER O., "*Callinectes* (Decapoda: Portunidae) larvae in the Middle Atlantic Bight, 1975-77" 251

Snapper, vermilion
reproductive biology, North and South Carolina
fecundity 142
maturation 140, 144
seasonality, frequency, and duration of spawning .. 139
sex ratio 141, 144

Sole, butter
eggs and larvae off Oregon and Washington
features, distinguishing 403
identification verification 403
morphology 405, 408
occurrence 412
ossification of meristic structures 409
pigmentation 404, 405

"Some statistical considerations of the design of trawl surveys for rockfish (Scorpaenidae)," by William H. Lenarz and Peter B. Adams 659

South Carolina
snapper, vermilion
reproductive biology 137

"Southern distribution of the Atlantic whitesided dolphin, *Lagenorhynchus acutus*, in the western North Atlantic," by Salvatore A. Testaverde and James G. Mead 167

"Spawn and larvae of the Pacific sandfish, *Trichodon trichodon*," by Jeffrey B. Marliave 959

Spawning
daily time of in the Peconic Bays, New York 455

"Spawning and fecundity of Atlantic mackerel, *Scomber scombrus*, in the Middle Atlantic Bight," by Wallace W. Morse 103

"Spawning and sexual maturity of Gulf menhaden, *Brevoortia patronus*," by Robert M. Lewis and Charles M. Roithmayr 947

"Spawning biomass and early life of northern anchovy, *Engraulis mordax*, in the northern subpopulation off Oregon and Washington," by Sally L. Richardson 855

"Species of *Munidopsis* (Crustacea, Galatheidae) occurring off Oregon and in adjacent waters," by Julie W. Ambler 13

Spot
Cape Fear River, North Carolina
retention of postlarval in tidal estuary 419
egg and larval development
body proportions 704
distinguishing from other sciaenids 712
embryonic development 702
fins 705
pigmentation 710
pterygiophore development and arrangements 709

Squid, long-finned
reproductive behavior, in situ observations 947

Squilla empusa
larval ecology in Chesapeake Bay
Cape Henry survey 694
research applied to national needs (RANN) survey 694
seasonal occurrence 695
temperature and salinity tolerence 697

Steelhead
production and growth of subyearling in Orwell Brook, New York 549
smolts, transportation in Columbia River and effects on adult returns
collection and marketing of fish and fish hauling procedures 493
comparison of results with other studies 502
effect of transportation on homing 503
evaluation of returning adults 494
experimental design 493
factors influencing assessment of data 494
percentage adult returns of transported releases .. 498
recovery of marked in the Indian and sport fisheries 501
returns of adult experimental fish to hatcheries and spawning grounds 501
returns of adult experimental fish to Little Goose Dam 496
size and years-in-ocean of adult experimental fish . 500
straying of experimental groups 502

STEIN, DAVID L.—see MATARESE and STEIN

Stellifer lanceolatus—see Drum, star

Stenella attenuata—see Dolphin, spotted

Stenella longirostris—see Dolphin, spinner

"Stomach contents and feces as indicators of harbor seal, *Phoca vitulina*, foods in the Gulf of Alaska," by Kenneth W. Pitcher 797

STONE, JAMES H.—see BISHOP et al.

STONER, ALLAN W., "Feeding ecology of *Lagodon rhomboides* (Pisces: Sparidae): Variation and functional responses" 337

STOUT, VIRGINIA F., "Organochlorine residues in fishes from the northwest Atlantic Ocean and Gulf of Mexico" 51

STRONG, CRAIG S.—see AINLEY et al.

STROUD, RICHARD K., CLIFFORD H. FISCUS, and HIROSHI KAJIMURA, "Food of the Pacific white-sided dolphin, *Lagenorhynchus obliquidens*, Dall's porpoise, *Phocoenoides dalli*, and northern fur seal, *Callorhinus ursinus*, off California and Washington" 951

SUGARMAN, PETER C.—see PEARSON et al.

"Summer food of Pacific cod, *Gadus macrocephalus*, in coastal waters of southeastern Alaska," by David M. Clausen 968

"(A) survey of ciguatera at Enewetak and Bikini, Marshall Islands, with notes on the systematics and food habits of ciguatoxic fishes," by John E. Randall 201

"Survival, size, and emergence of pink salmon, *Oncorhynchus gorbuscha*, alevins after short- and long-term exposures to ammonia," by Stanley D. Rice and Jack E. Bailey 641

"Systematics and distribution of ceratioid anglerfishes of the family Melanocetidae with the description of a new species from the eastern North Pacific Ocean," by Theodore W. Pietsch and John P. Van Duzer 59

TAYLOR, SIDNEY G.—see BAILEY et al.

"Temperature effects on growth and yolk utilization in yellowtail flounder, *Limanda ferruginea*, yolk-sac larvae," by W. Huntting Howell 731

TESTAVERDE, SALVATORE A., and JAMES G. MEAD, "Southern distribution of the Atlantic white-sided dolphin, *Lagenorhynchus acutus*, in the western North Atlantic" 167

Texas, southern
  dolphin, bottlenose
    occurrence, movements, and distribution 593

THEILACKER, GAIL H., "Changes in body measurements of larval northern anchovy, *Engraulis mordax*, and other fishes due to handling and preservation" 685

THEILACKER, GAIL H., "Rearing container size affects morphology and nutritional condition of larval jack mackerel, *Trachurus symmetricus*" 789

Theragra chalcogramma—see Pollock, walleye

Thunnus thynnus—see Tuna, bluefin

Tomcod, Atlantic
  observations on early life stages
    developmental stages 150
    dry weight 153
    egg collection 148
    egg diameter 153
    field observations 150
    field studies 147
    laboratory studies 148
    specific gravity 152
    specific gravity of egg solids 154
    statistical procedures 149
    survival to hatch and length at hatching 152
    water content 152

Tomcod, Pacific
  larval development in northeast Pacific Ocean
    comparative notes on *Theragra chalcogramma* and *Gadus macrocephalus* 935
    fins 931
    head and axial skeleton 929
    identification 925
    measurements 924
    morphology 929
    occurrence 935
    pigment patterns 925
    scales 935
    specimens 924

Trachurus symmetricus—see Mackerel, jack

"Transportation of chinook salmon, *Oncorhynchus tshawytscha*, and steelhead, *Salmo gairdneri*, smolts in the Columbia River and effects on adult returns," by Wesley J. Ebel 491

Trawl, beam
  wheels, metering
    effectiveness for measurement of area sampled 791

Trawl, midwater nekton
  compared with Isaacs-Kidd midwater trawl
    effective cross-sectional area of the pelagic trawl .. 533
    flushing of the pelagic trawl 531
    length-frequency comparisons 532
    midwater trawl description and operation 529
    pelagic trawl-IKMT comparisons 532

Trichodon trichodon—see Sandfish, Pacific

Trimethylamine
  improved method to analyze in fish
    cold method of analysis for TMA 472
    comparative analyses using fish flesh 470
    extraction of fish flesh with added TMA and DMA . 471
    extraction of TMA 470
    extraction procedure for fish flesh 466
    purification procedures 466
    reaction of ammonia 467
    reaction of DMA 468
    TMA, methods of analyses 466

Tuna, bluefin
  Atlantic Ocean
    shedding rates of plastic and metal dart tags 179

Tursiops truncatus—see Dolphin, bottlenose

Turtle, Atlantic ridley
  radiologic method for examination of gastrointestinal tract 965

Turtle, loggerhead
  radiologic method for examination of gastrointestinal

tract 965

United States
fish meal demand analysis 267

"Use of Griffin's yield model for the Gulf of Mexico shrimp fishery," by Arvind Khilnani 973

"Using Box-Jenkins models to forecast fishery dynamics: Identification, estimation, and checking," by Roy Mendelssohn 887

"Using Markov decision models and related techniques for purposes other than simple optimization: Analyzing the consequences of policy alternatives on the management of salmon runs," by Roy Mendelssohn 35

VAN DUZER, JOHN P.—see PIETSCH and VAN DUZER

VERITY, PETER G.—see DURBIN et al.

"Voluntary swimming speeds and respiration rates of a filter-feeding planktivore, the Atlantic menhaden, *Brevoortia tyrannus* (Pisces: Clupeidae)," by Ann G. Durbin, Edward G. Durbin, Peter G. Verity, and Thomas J. Smayda 877

Washington
anchovy, northern
reproduction off 603
spawning biomass and early life in northern subpopulation 855
food of Pacific white-sided dolphin, Dall's porpoise, and northern fur seal off 951
sole, butter
eggs and larvae off 401

Water currents
influence of on daily foraging movements of blacksmith 829

WEIHS, DANIEL, "Respiration and depth control as possible reasons for swimming of northern anchovy, *Engraulis mordax*, yolk-sac larvae" 109

WEINSTEIN, MICHAEL P., SIDNEY L. WEISS, RONALD G. HODSON, and LAWRENCE R. GERRY, "Retention of three taxa of postlarval fishes in an intensively flushed tidal estuary, Cape Fear River, North Carolina" 419

WEIS, JUDITH SHULMAN—see WEIS and WEIS

WEIS, PEDDRICK, and JUDITH SHULMAN WEIS, "Effect of zinc on fin regeneration in the mummichog, *Fundulus heteroclitus*, and its interaction with methylmercury" 163

WEISS, SIDNEY L.—see WEINSTEIN et al.

WELLS, RANDALL S.—see MEAD et al.

Whale, bowhead
estimated initial population size of Bering Sea stock
aspects of fishery 852
catch history 845
data limitations 850
estimates of current stock size 845
estimates of initial stock size 845
lag time 847
model development 847
model limitations 851
natural mortality 847
net recruitment rate 847
recovery times 850
risk analysis 848
vital parameters 850

Whale, false killer
recurrent mass stranding in Florida
behavior in captivity 174
hematology 174
relationships among strandings 175
sequence of events 171

Wheels, metering
effectiveness for measurement of area sampled by beam trawls
consistency with other estimates of distance 794
count consistency 793
wheel counts versus catch data 794

WINGERT, R. CRAIG—see QUINN et al.

WOODRUFF, DANA L.—see PEARSON et al.

Zooplankton
influence of density on daily foraging movements of blacksmith 829

INFORMATION FOR CONTRIBUTORS TO THE *FISHERY BULLETIN*

Manuscripts submitted to the *Fishery Bulletin* will reach print faster if they conform to the following instructions. These are not absolute requirements, of course, but desiderata.

CONTENT OF MANUSCRIPT

The **title page** should give only the title of the paper, the author's name, his affiliation, and mailing address, including ZIP code.

The **abstract** should not exceed one double-spaced page.

In the **text,** *Fishery Bulletin* style, for the most part, follows that of the *U.S. Government Printing Office Style Manual*. Fish names follow the style of the American Fisheries Society Special Publication No. 6, *A List of Common and Scientific Names of Fishes from the United States and Canada,* Third Edition, 1970.

Text footnotes should be typed separately from the text.

Figures and **tables,** with their legends and headings, should be self-explanatory, not requiring reference to the text. Their placement should be indicated in the right-hand margin of the manuscript.

Preferably **figures** should be reduced by photography to 5¾ inches (for single-column figures, allowing for 50% reduction in printing), or to 12 inches (for double-column figures). The maximum height, for either width, is 14 inches. Photographs should be printed on glossy paper.

Do not send original drawings to the Scientific Editor; if they, rather than the photographic reductions, are needed by the printer, the Scientific Publications Office will request them.

Each **table** should start on a separate page. Consistency in headings and format is desirable. Vertical rules should be avoided, as they make the tables more expensive to print. Footnotes in tables should be numbered sequentially in arabic numerals. To avoid confusion with powers, they should be placed to the *left* of numerals.

Acknowledgments, if included, are placed at the end of the text.

Literature is cited in the text as: Lynn and Reid (1968) or (Lynn and Reid 1968). All papers referred to in the text should be listed alphabetically by the senior author's surname under the heading "Literature Cited." Only the author's surname and initials are required in the **literature cited.** The accuracy of the **literature cited** is the responsibility of the author. Abbreviations of names of periodicals and serials should conform to *Biological Abstracts List of Serials with Title Abbreviations. (Chemical Abstracts* also uses this system, which was developed by the American Standards Association.)

Common **abbreviations** and **symbols,** such as mm, m, g, ml, mg, ° C (for Celsius), %, ‰ and so forth, should be used. Abbreviate units of measure only when used with numerals. Periods are only rarely used with abbreviations.

We prefer that **measurements** be given in metric units; other equivalent units may be given in parentheses.

FORM OF THE MANUSCRIPT

The original of the manuscript should be typed, double-spaced, on white bond paper. Please triple space above headings. We would rather receive good duplicated copies of manuscripts than carbon copies. The sequence of the material should be:

TITLE PAGE
ABSTRACT
TEXT
LITERATURE CITED
APPENDIX
TEXT FOOTNOTES
TABLES (Each table should be numbered with an arabic numeral and heading provided)
LIST OF FIGURES (Entire figure legends)
FIGURES (Each figure should be numbered with an arabic numeral; legends are desired)

ADDITIONAL INFORMATION

Send the ribbon copy and two duplicated or carbon copies of the manuscript to:

Dr. Carl J. Sindermann, Scientific Editor
Fishery Bulletin
Northeast Fisheries Center
Sandy Hook Laboratory
National Marine Fisheries Service, NOAA
Highlands, NJ 07732

Fifty **separates** will be supplied to an author free of charge and 100 supplied to his organization. No covers will be supplied.

STROUD, RICHARD K., CLIFFORD H. FISCUS, and HIROSHI KAJIMURA. Food of the Pacific white-sided dolphin, *Lagenorhynchus obliquidens*, Dall's porpoise, *Phocoenoides dalli*, and northern fur seal, *Callorhinus ursinus*, off California and Washington 951
MARLIAVE, JEFFREY B. Spawn and larvae of the Pacific sandfish, *Trichodon trichodon* 959
McCLELLAN, G. L., and J. K. LEONG. A radiologic method for examination of the gastrointestinal tract in the Atlantic ridley, *Lepidochelys kempi*, and loggerhead, *Caretta caretta*, marine turtles 965
CLAUSEN, DAVID M. Summer food of Pacific cod, *Gadus macrocephalus*, in coastal waters of southeastern Alaska 968
KHILNANI, ARVIND. Use of Griffin's yield model for the Gulf of Mexico shrimp fishery 973
GOLDBERG, STEPHEN R. Seasonal spawning cycle of the Pacific butterfish, *Peprilus simillimus* (Stromateidae) 977
DAVIS, GARY E. Effects of injuries on spiny lobster, *Panulirus argus*, and implications for fishery management 979

INDEX, VOLUME 78 985

☆ GPO 696-404

NORTHEAST
LIBRARY BINDING CO. INC.
DEC 1991
MEDFORD, MASS.

MBL/WHOI LIBRARY
WH 1905 A